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THE BREEDING RANGE OF THE BARROW'S GOLDENEYE IN EASTERN NORTH AMERICA

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ABSTRACT.—The breeding range of Barrow's Goldeneye (*Bucephala islandica*) is largely restricted to northwestern North America, and little is known of the small population that winters in eastern Canada. Based on weak evidence, this eastern population was thought to nest mainly in northern Labrador. Our May 1990 to 1998 surveys identified a breeding area in the forest regions of the Quebec Laurentian Highlands. We observed Barrow's Goldeneyes on 137 lakes and 5 rivers, of which 95.2% were along the north shore of the St. Lawrence estuary and gulf. The species was found mainly on small lakes (≤ 10 ha) at greater than 500 m elevation. Most occupied lakes (96.5%) were within 100 km of the St. Lawrence River and 48.9% of them were headwater lakes. Four broods observed in 1998 represent the first eastern North American documentation of breeding. By means of satellite telemetry, 5 of 7 males captured on the wintering grounds were relocated on the north shore of the St. Lawrence River in May, 60–140 km inland from the estuary and gulf. Each male spent 34–50 days at its respective site, presumably with a mate. The north shore of the estuary and gulf may be the core breeding area for Barrow's Goldeneyes wintering along the St. Lawrence River. *Received 29 March 1999, accepted 4 Sept. 1999.*

The breeding range of Barrow's Goldeneye (*Bucephala islandica*) is largely restricted to northwestern North America, where more than 90% of the world population (ca 150,000–200,000) breeds from central Alaska to northern California (del Hoyo et al. 1992; Eadie et al., in press). Elsewhere, the species breeds in Iceland, where the spring population is estimated at 2000 birds and most individuals are sedentary (Scott and Rose 1996, Hagemeijer and Blair 1997). A single breeding observation was recorded in Greenland in the nineteenth century; however, no observations have been reported for at least the last 30 years (Boertmann 1994). A few thousand Barrow's Goldeneyes are known to winter in northeastern North America, particularly in the St. Lawrence estuary, Quebec (Reed and Bourget 1977, Savard 1990), and a breeding population has recently been suspected in southern Quebec (Savard and Cormier 1995; Gauthier and Aubry 1996; Savard and Dupuis, in press). Many authors (e.g., Palmer 1976, Bellrose 1980, Godfrey 1986, del Hoyo et al. 1992, American Ornithologists' Union 1998) state that the species breeds in northern Labrador and southwestern Greenland but there is little documentation and some of the records have been disputed (Todd 1963). Apparently, as suggested by Scott and Rose (1996) and Hagemeijer and Blair (1997), the assumption is that the Barrow's Goldeneyes wintering in

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the St. Lawrence estuary and elsewhere in Atlantic Canada and the U.S. originate from these Arctic breeding areas.

We conducted surveys and tracked movements of Barrow's Goldeneyes using satellite telemetry because of growing concern about the vulnerability of the eastern population of this species (Gauthier and Aubry 1996; Savard and Robert 1997; Savard and Dupuis, in press) and because of the lack of information about their distribution. Here, we (1) document the first breeding records of the Barrow's Goldeneye in eastern North America, (2) describe the breeding distribution based on inland surveys and satellite telemetry, and (3) discuss the types of lakes where we found the species.

METHODS

Helicopter surveys.—Inland observations of Barrow's Goldeneyes were obtained from helicopter surveys conducted by the Black Duck Joint Venture (BDJV) of the North American Waterfowl Management Plan (Anonymous 1986, 1994). Each May 1990–1998, BDJV surveys in Quebec covered about 500,000 km^2 in the Boreal Shield and Atlantic Maritime ecozones (Wiken 1986) south of 51° 30′ N. In 1990–1992, an original set of 83 100 km^2 (10 km × 10 km) quadrats systematically distributed over that area were annually surveyed. In 1993–1995, the number of quadrats was gradually decreased to 35 (50 in 1993, 43 in 1994, and 35 in 1995), all being randomly selected from the original set of 83. In 1996–1998, quadrat size was reduced to 25 km^2 (5 km × 5 km), but the number was increased to 156, half of them being randomly surveyed each year. Many 25 km^2 quadrats were located in the southwest quarter of the 83 original 100 km^2 quadrats to ensure continuity in the data set. Within each quadrat, the helicopter (Bell 206 L) flew over the margins of all aquatic habitats and all waterfowl were noted by three observers. Flight speed varied from 50 to 100 km/h, and altitude from 5 to 50 m, depending on the complexity of aquatic habitats and topography. All waterfowl observations were located on 1:50,000 topographic maps during the survey and later entered into georeferenced databases. Barrow's were distinguished from Common Goldeneyes (*Bucephala clangula*) by the distinctive, darker upperwing pattern of adult males (Tobish 1986) or, more rarely, by their facial crescent.

We conducted 2 additional helicopter surveys of Barrow's Goldeneyes in 1998. The first on 14–15 May to verify the presence inland of 2 males fitted with transmitters (see below) and to survey a few lakes located in the vicinity of these radio-tracked individuals. The second on 17 May was conducted over a 252 km^2 area 60 km inland northwest of Sept-Îles (66° 50′ W, 51° 47′ N), in which all 190 lakes were overflown in the same way as for BDJV surveys. Lakes with Barrow's Goldeneye sightings were resurveyed in July to locate broods (Morneau 1998). Barrow's Goldeneye females were distinguished from Common Goldeneyes by their distinctive head and bill shapes and head color (Tobish 1986).

Ground surveys.—From 20 May to 4 June 1998, we surveyed Barrow's Goldeneyes on 34 accessible lakes in the controlled hunting zone ZEC Martin-Valin and 68 lakes in ZEC Chauvin. Both hunting zones are located about 60 km northwest of the mouth of the Saguenay River (69° 43′ W, 48° 09′ N). Each lake was surveyed at least once, using binoculars and a spotting scope. All lakes with Barrow's Goldeneyes were revisited at least once between 30 June and 8 July to locate broods.

Statistics.—Unless otherwise specified, all means are shown with their standard error. We used Microsoft Excel 7.0a for Windows 95 for statistical analysis.

Satellite telemetry.—We implanted satellite transmitters in 7 Barrow's Goldeneye drakes (Korschgen et al. 1996). We used Argos PTT-100 implant transmitters (Microwave Telemetry, Columbia, Maryland) that weighed about 51 g (4.6% or less of the body weight). Each transmitter had 4 lithium batteries, was L-shaped, measured about 57 mm long, 36 mm wide, and 15 mm deep on its deepest side (7.5 mm on the other), and had a 22 cm antenna made of Teflon-coated multistrand stainless steel wire. We used a mobile surgical unit, including a portable anesthetic machine (Labvet, Dispomed Ltd., Joliette, Quebec) because we had to work in remote locations. We modified the procedure of Korschgen and coworkers (1996) for the surgery. Transmitters were gas sterilized (ethylene oxide at 38° C) and surgical instruments were autoclaved prior to field work. Each goldeneye was induced using a face mask (customized with a plastic cup) with a concentration of 3.5–4.0% isoflurane (Aerrane, Janssen, Mississauga, Ontario) delivered in oxygen. The bird was then intubated with a non-cuffed 3.5-mm endotracheal tube (Murphy's type, Portex, London, U.K.) to maintain anesthesia with a concentration of 2.5–3.0% isoflurane. A transparent surgical drape (Veterinary Specialty Products, Boca Raton, Florida) was used to cover the bird. The anesthetized bird was monitored with an ultrasonic Doppler flow detector (Medical Electronics Model 811-B, Parks, Alòha, Oregon) installed at the base of the tongue, and a respiration monitor (Tidal Volume Monitor, Medical Engineering & Development, Jackson, Michigan). Two veterinarians performed the procedure, one surgeon and one anesthetist, while a third person was available for technical help.

All birds (n = 7) were captured along the north shore of the St. Lawrence estuary, Quebec. We captured 3 adult males on 21–22 February 1998 at Baie-des-Rochers (69° 48′ W, 47° 58′ N) and 4 others on 7–10 April 1998 at Mistassini (67° 57′ W, 49° 17′ N). These two localities lie 170 km and 380 km downstream from Quebec City, respectively. Birds were attracted with Barrow's Goldeneye decoys ($n \geq 20$) and captured using two 18 m mist nets (127 mm mesh size) set side by side over water, with three rafts similar to, but stronger than, the 'shallow-water system' described by Burns and coworkers (1995). Birds were transported and held in pierced plastic boxes (54 × 34 × 42 cm) in which paper strips were placed and changed regularly to avoid feather damage or contamination with droppings, or respiratory stress (from overwhelming dust or *Aspergillus* spores). Average time between capture and release after surgery was 5 h 42 min ± 36 min (range = 3 h 40 min–7 h 45 min). The surgical procedure, from incision to closure, was completed on average in 44 min ± 2 (range = 36–51). Birds were released to the wild on average 1 h 58 min ± 24 min (range = 1 h 15 min–4 h 1 min) after the end of anesthesia. To avoid long-term stress no duck was held overnight. Although we were not able to monitor each duck after its release, we observed no abnormal behavior attributable to the surgery.

Lake characteristics and distribution.—We used topographic maps (scale 1:50,000) to measure the area, perimeter, and elevation of each lake used by Barrow's Goldeneyes, and to determine whether the lake was a headwater lake. We calculated the shortest distance between each lake and the St. Lawrence River using digital maps (scale 1:2,500,000; Geomatics Canada).

Abundance map.—An abundance map of Barrow's Goldeneye pairs was constructed from the BDJV helicopter surveys to illustrate the species' breeding distribution in southern Quebec. To combine the 9 years of data, we first calculated annual densities of indicated pairs per 100 km^2 for all quadrats (either 25 km^2 or 100 km^2). We then assigned to the coordinates of the center of all quadrats the maximum density of indicated pairs observed during any given year (each quadrat was surveyed from 1 to 7 years in 1990–1998). For each 25 km^2 quadrat that was part of a 100 km^2 quadrat, we used the center of the 25 km^2 quadrat and the maximum density irrespective of quadrat size, resulting in a total of 172 quadrats. Indicated pairs were estimated as follows: 1 or 2 birds = 1 pair, regardless of sex; otherwise = 0 pair (Bordage and Plante 1997). Because of the discrete nature of our data, we used the Inverse Distance Weighted interpolator (Environmental Systems Research Institute Inc., ArcView Spatial Analyst) based on a radius of 60 km to produce a continuous representation of the various density classes. Because quadrat centers were 50 km apart, the interpolation used as many as 4 neighboring quadrats.

RESULTS

Helicopter surveys.—From 1990 to 1998, 222 Barrow's Goldeneyes (129 males and 93 females, from a total of 118 observations) were identified during Black Duck Joint Venture surveys. Nearly all were located inland from the north shore of the St. Lawrence estuary and gulf on lakes (n = 96) and rivers (n = 5). Indicated pairs (n = 108) mostly consisted of lone pairs (n = 66) and lone males (n = 35); all were observed between 10 May and 1 June. We located 2 of the males fitted with transmitters during surveys conducted on 14–15 May 1998; neither was accompanied by a female. A survey of the lakes in the vicinity of these 2 radio-tracked individuals yielded 17 other Barrow's Goldeneyes: 8 pairs and 1 lone male on 8 lakes. The survey conducted 60 km northwest of Sept-Îles in 1998 yielded 8 pairs and 1 lone male distributed on 6 lakes. During brood surveys on these same lakes, we observed 3 broods (13–14 July) and 1 lone female (16 July). Based on an incubation period of 30 days (Eadie et al., in press) and duckling age, we estimated that the 3 females with broods began incubation on 23 May, 2 June, and 10 June.

Ground surveys.—During spring surveys conducted north of the Saguenay River, we observed 36 Barrow's Goldeneyes on 23 lakes. Five lakes were in ZEC Martin-Valin and 18 were in ZEC Chauvin. Most observations were of lone pairs (n = 12) or lone males (n = 9). Subsequent surveys led to the discovery of 1 female accompanied by a brood on 2 July (photo in Bannon et al. 1998) and 7 lone females on 2–7 July. We estimated that the female with a brood began incubation on 30 May.

Satellite telemetry.—Beginning in the last week of April, 5 males moved 60–140 km [$\bar{x}$ = 84 ± 34 (SD)] inland along the north shore of the St. Lawrence estuary and gulf, between the mouth of the Saguenay River and Mingan (Fig. 1). They spent a minimum average of 44 days (±6; range = 3–50) at their respective sites, presumably with their mates. The other 2 males stayed along the St. Lawrence River, where they were located until 5 June and 22 June 1998, respectively.

Lake characteristics and distribution.—Overall, we observed Barrow's Goldeneyes on 137 lakes and 5 rivers, 95.2% of which were along the north shore of the St. Lawrence estuary and gulf. Although birds were observed on lakes from 0.2 to 799.1 ha in size (26.4 ha ± 82.3; median = 5.3 ha; n = 137), most were found on small lakes with 45.6% and 69.9% of lakes occupied by Barrow's Goldeneyes being less than 5 ha and 10 ha, respectively. Lakes and rivers with Barrow's Goldeneyes were at a mean eleva-

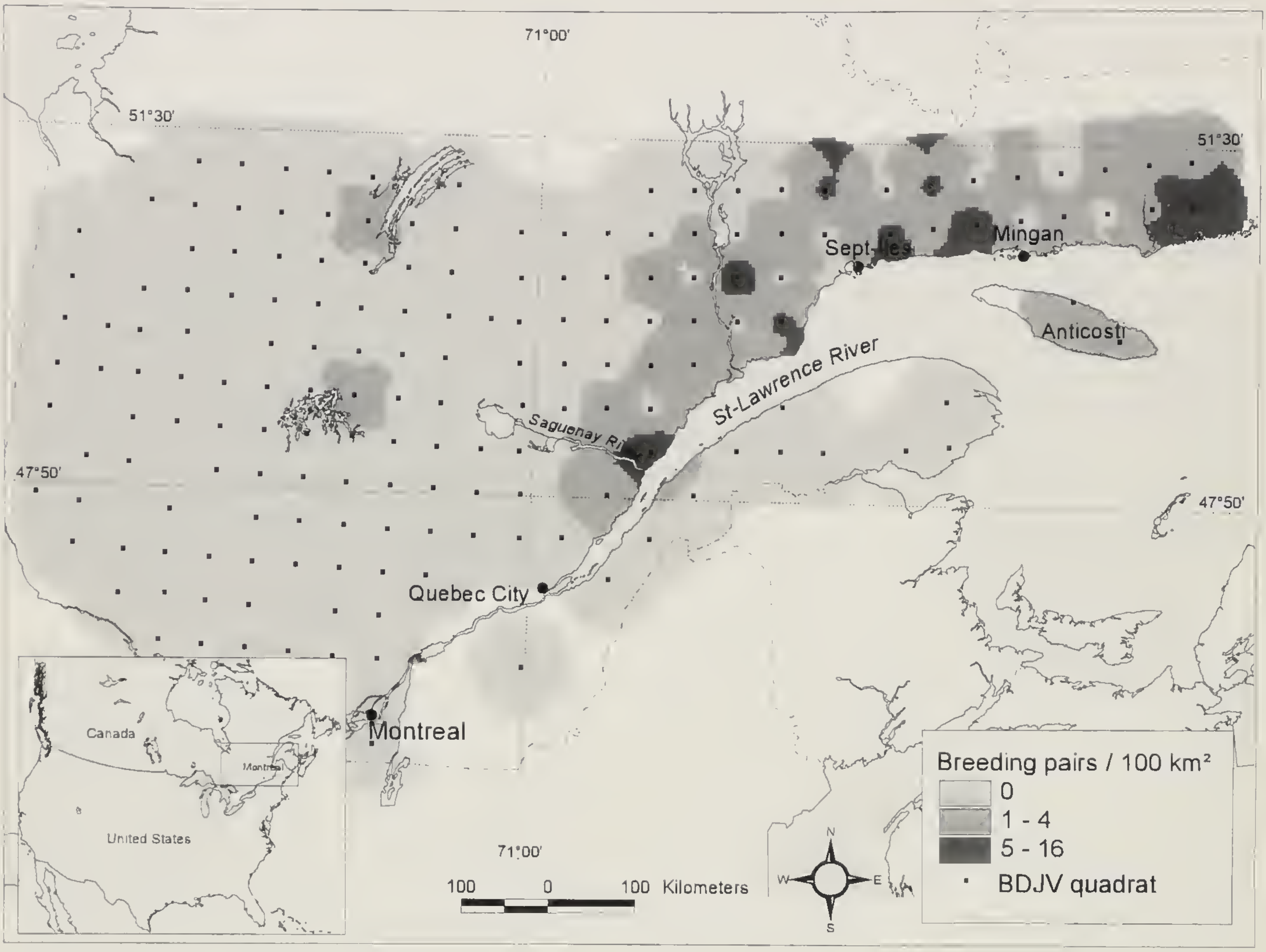

FIG. 1. Location of Black Duck Joint Venture (BDJV) survey quadrats and estimated breeding densities of Barrow's Goldeneyes in southern Quebec.

tion of 489 m (±187; median = 518 m; range = 100–792; *n* = 142), with 54.2% and 29.6% of them above 500 m and 600 m, respectively. Almost half (48.9%) were headwater lakes. Few Barrow's Goldeneyes were located far from the St. Lawrence River; nearly all occupied lakes and rivers (96.5%) were within 100 km of it (70.1 km ± 53; range = 13–430; *n* = 142).

Abundance map.—Indicated breeding pairs were observed on 27 of 172 of BDJV quadrats, 25 of these were north of the St. Lawrence River (Fig. 1). We delineated a 'core breeding area' north of 47° 50′ N and east of 71° W where we observed indicated pairs in 25 of 47 of the quadrats surveyed. Only 2 indicated breeding pairs were recorded outside this area. The highest breeding pair densities were recorded on the Laurentian Highlands in quadrats closest to the St. Lawrence River.

DISCUSSION

Our observations of 4 different broods constitute the first documented breeding records of Barrow's Goldeneyes in eastern North America. The difficulty of positively identifying females and young goldeneyes in the field (Tobish 1986) and the remote nesting areas occupied by the species have certainly been responsible for the delay in establishing definite breeding records for this region. Given that the species breeds within 100 km of the St. Lawrence River, we think that some of the historical breeding records of the Barrow's Goldeneye on the north shore of the St. Lawrence disputed by Todd (1963) could well be valid. This could be the case for Merriam's (1881) and Salvadori's (1895) records. The 2 lone females shot by Todd himself on the St. Margaret River on 10 and 30 June 1917 (Todd 1963) could also have been nesting individuals based on the time they were collected (see also Comeau 1909). Other unsubstantiated breeding records have been reported in eastern North America. These include a 'probable' female Barrow's Goldeneye with 9 young reported in the Torrent River watershed area of Newfoundland in 1993 (Daury and Bateman 1996), and a nest collected in 1886 on the coast of Newfoundland originally identified as a Barrow's Goldeneye nest by its collector (Western Foundation of Vertebrate Zoology, #90022). However, according to egg measurements (R. Corado, pers. comm.), and knowing the difficulty of distinguishing between Barrow's and Common goldeneye females (especially during the nineteenth century), we think the latter record could have been a Common Goldeneye nest.

Based on our satellite tracking, at least some of the Barrow's Goldeneyes wintering along the St. Lawrence River breed along the north shore of the estuary and gulf. In fact, the large numbers of pairs and lone males we detected in aerial and ground surveys indicate that this area may be the core breeding area for the 2000–4000 (Reed and Bourget 1977; Savard and Dupuis, in press) Barrow's Goldeneyes wintering along the St. Lawrence. Because of this, we question the assumption that Barrow's Goldeneyes wintering in Quebec and elsewhere in Atlantic Canada and the U.S. originate from Arctic breeding areas (see Scott and Rose 1996, Hagemeijer and Blair 1997). In our view, the north shore inland from the St. Lawrence estuary and gulf represents a sizable breeding area that can account for most, if not all, of the Barrow's Goldeneyes wintering in Quebec. Because of this, we also believe that the status of the Barrow's Goldeneye in northern (Arctic) Labrador and Quebec requires further investigation. According to Palmer (1976), the species breeds near or along the upper half of the Labrador coast and is probably an occasional nester inland at least in northern Ungava. Todd (1963) reported various records of adults and young, and mentioned L. M. Tuck as having collected specimens, including juveniles, at various points along the Labrador coast. 'Probable' Barrow's Goldeneye eggs were also collected in 1887 from a nest found on the coast of Labrador (Western Foundation of Vertebrate Zoology, #123700; R. Corado, pers. comm.). The species may also breed in the Hudson Bay area (Todd 1963, Gauthier and Aubry 1996). Nevertheless, it is quite possible that some of the northern observations were of birds migrating to their molting sites because Barrow's Goldeneyes molt in Hudson Bay, Ungava Bay, and in some fjords of northern Labrador (C.W.S., unpubl. data). Obviously, the breeding of Barrow's Goldeneyes in treeless Arctic environments of eastern North America needs to be better documented.

Most Barrow's Goldeneyes were observed east of the Saguenay River and north of the St. Lawrence estuary and gulf, with the highest densities in the southern portion of the Laurentian Highlands. Generally, birds were found in the Boreal ecoclimatic province of Quebec, in the black spruce (*Picea mariana*)-feather moss (Hypnaceae) and balsam fir (*Abies balsamea*)-white birch (*Betula papyrifera*) forest regions (sensu Gauthier and Aubry 1996). Although no survey quadrats were located within 30 km of the St. Lawrence River, we suspect that Barrow's Goldeneyes are unlikely to breed there. This area corresponds to the East St. Lawrence lowlands (sensu Gauthier and Aubry 1996), is at sea level, and contrasts markedly with the high elevation habitat where we found most pairs of Barrow's Goldeneyes. Breeding pairs observed west of 71° W and on Anticosti Island were all single year observations indicating that these individuals may have been migrating. Indeed, despite extensive field studies on Anticosti Island (Ouellet 1969, Gauthier and Aubry 1996), no breeding Barrow's Goldeneye has been confirmed.

Our results clearly indicate that the respective breeding ranges of Barrow's and Common goldeneyes (Gauthier and Aubry 1996) are not mutually complementary in eastern North America as suggested by Todd (1963). He associated the former with the treeless areas of the Arctic and the latter with forested areas. On the contrary, our study indicates that these two species have sympatric distributions, at least in some parts of the boreal forest of eastern Quebec. There might be a segregation of the two species based on elevation. In southern Quebec, the mean elevation increases east of the Saguenay River (Ecological Stratification Working Group 1995), which corresponds to the western limit of the core breeding distribution of Barrow's Goldeneyes.

In fact, it is clear that most Barrow's Goldeneyes are associated with high elevation lakes and are rarely found on low elevation lakes. The Common Goldeneye commonly occurs on low elevation lakes (D.B., pers. obs.), but its abundance on high elevation lakes remains to be verified. Such segregation of the two species has been documented in the Columbia Valley, British Columbia (Savard 1984). There, Barrow's Goldeneyes were restricted to the alkaline ponds of the plateaus, whereas Common Goldeneyes were most numerous on the freshwater valley ponds. Definitively, a comparative study of the two species of goldeneyes is needed in eastern North America.

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THE DIET OF STELLER'S EIDERS WINTERING IN VARANGERFJORD, NORTHERN NORWAY

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ABSTRACT.—We examined the winter diet of Steller's Eiders (*Polysticta stelleri*) in Varangerfjord, northern Norway, by analyzing the esophagus content of 29 individuals (12 juveniles and 17 adults). A total of 8389 prey items of 31 species were identified: 13 species of gastropods (making up 68.4% of total number of items); 4 species of bivalves (18.5%); 12 species of crustaceans (13%); and 2 species of echinoderms (<0.1%). In terms of percentage aggregate wet weight 31.4% was gastropods, 22.6% was bivalves, and 41.4% was crustaceans. Juvenile eiders ate more crustaceans ($\bar{x}$ = 61% aggregate w.w.) than adults ($\bar{x}$ = 26%, $P < 0.05$), possibly because they were in poor body condition and may have had higher energy requirements than adults. Adults tended to eat more gastropods ($\bar{x}$ = 41% vs 22%) and *Mytilus edulis* ($\bar{x}$ = 27% vs 12%) than juveniles. There were only small differences between sexes. Most of the prey items were of species known to be associated with kelp plants, especially *Laminaria hyperborea*, suggesting that Steller's Eiders obtain a large proportion of their prey directly from the vegetation. *Received 16 April 1999, accepted 19 Oct. 1999.*

The winter diets of most sea ducks (tribe Mergini and Somaterini) are well known, but not for the Steller's Eider (*Polysticta stelleri*). This species inhabits remote areas, breeding along the Arctic coasts of Siberia and Alaska and wintering in sub-arctic waters in Alaska, East-Asia, and northwestern Europe. About 15–25% (30,000–50,000 birds) of the world population winters in northwestern Europe, most (> 80%) in Varangerfjord in northeastern Norway and along the coast of the Kola Peninsula in northwestern Russia (Nygård et al. 1995). North American researchers that have quantified the diet of the Steller's Eider during the breeding season (Cottam 1939), molt (Petersen 1980, 1981), and winter (Metzner 1993) have found that it consists mostly of small gastropods, bivalves, and crustaceans. In northwestern Europe the diet of the species is poorly known (Siivonen 1941, Mitchell et al. 1996). Here we present quantitative information on the diet of the population wintering in Varangerfjord.

METHODS

Study area.—The study area was on the northern side of Varangerfjord (Fig. 1). The area consists of shoreline dominated by gently shelving coastal profiles with shallow water (<50 m) that may extend several km out from the shore (Fox and Mitchell 1997). The benthic communities in this area are dominated by large beds of kelp, especially *Laminaria hyperborea* (Bustnes and Systad, unpubl. data). Flocks consisting of both juvenile and adult eiders, of both sexes fed by diving in shallow waters (< 5 m; Bustnes and Systad, unpubl. data). Steller's Eiders were collected during winter (late November to early April) in the area between Ekkerøy (70° 04′ N, 30° 05′ E) and Urdnes (70° 08′ N, 30° 15′ E; Fig. 1), from November 1996 until April 1998. Birds were shot during daylight hours using a shotgun from a small boat, or with a .22 caliber rifle from the shore.

All birds were aged and sexed using plumage characteristics (Palmer 1976) and the presence or absence of a bursa of Fabricius. They were either dissected on the same day that they were shot or frozen shortly after they had been killed. The esophagus (including the proventriculus) and gizzard were removed and their contents kept separate and frozen immediately after dissection. For the analyses, food items from the esophagus and proventriculus were combined, but kept separate from the gizzard contents. We excluded the gizzard from the analyses because its contents were fragmentary. The food items were identified to species whenever possible. The prey items were counted and weighed on a Precisa 100A-300M balance to the closest 0.001 g. Each species was weighed separately except for the crustaceans which were separated into amphipods and isopods. Some esophagi contained damaged crustaceans from which species or number of separate individuals could not be determined. This damaged matter was only used in the proportion aggregate wet weight of the total of crustaceans and not included in the total number of prey items.

Data were summarized as the proportion of the food total for all individuals (frequency of occurrence and wet weight) and the mean frequency and the mean

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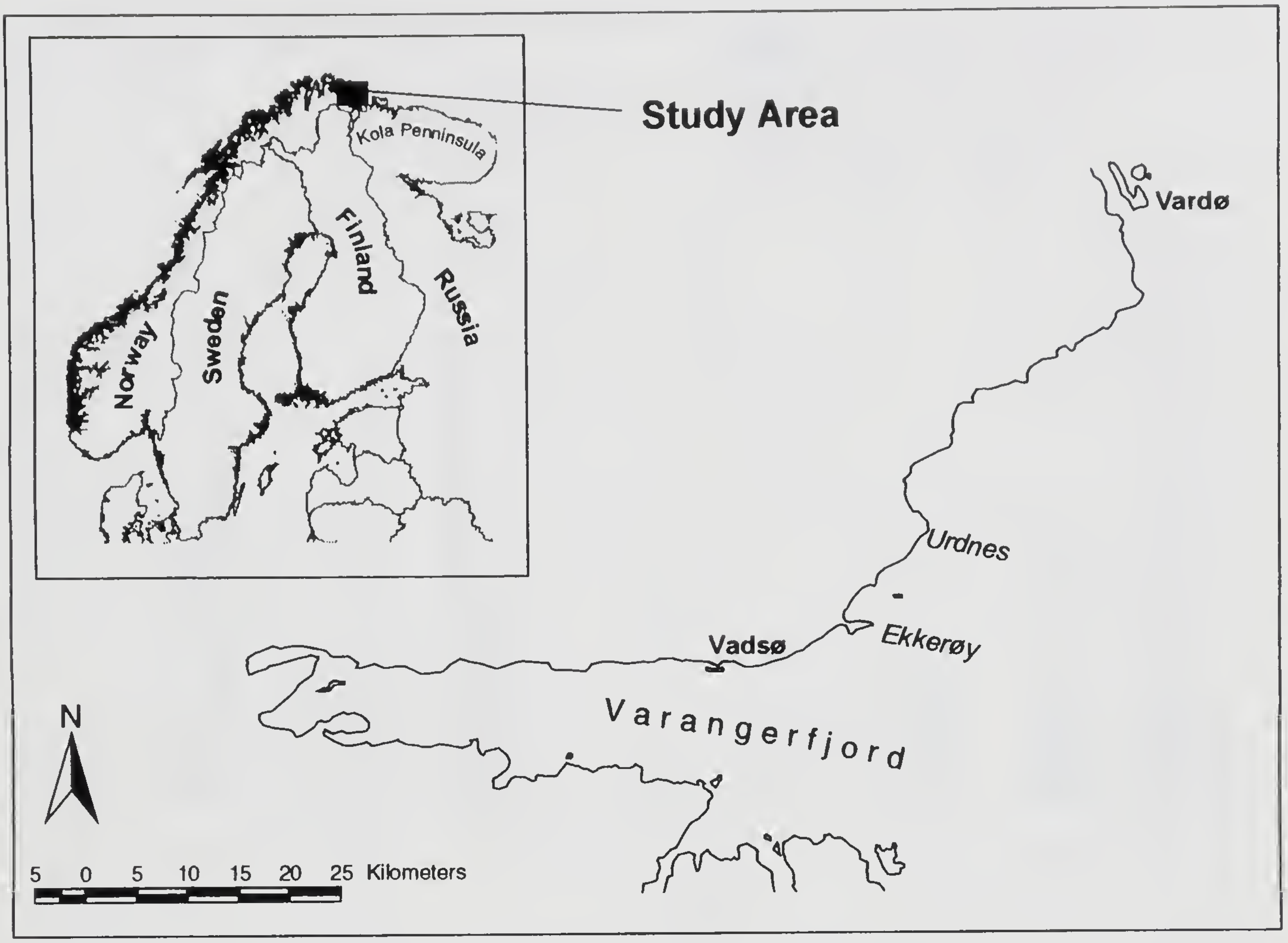

FIG. 1.—The study area in Varangerfjord, northern Norway.

aggregate percent wet weight among individuals (Table 1, see Krapu and Reinecke 1992 for a review).

Analyses.—We analyzed the proportions of aggregate wet weight using two-way ANOVAs (SAS, version 6.04 on an IBM PC; PROC GLM, SAS 1990). Because of lack of normality (tested by PROC UNIVARIATE) we used rank transformation (PROC RANK, SAS 1990; Conover and Iman 1981, Potvin and Roff 1993). Gastropods and crustaceans were pooled into groups and no species was analyzed individually. Among bivalves, only *Mytilus edulis* was a common prey of a large number of birds and was the only species we analyzed statistically. The dependent variable was the proportion of each prey type (wet weight of the prey type in question divided by the weight of the total prey content of each bird). Independent variables were sex and age of the bird. All models were tested for interactions, which were removed when not significant. Standard errors (SE) are given for all means. The sample consisted of 29 birds, 12 juveniles (6 males and 6 females) and 17 adults (11 males and 6 females).

RESULTS

Thirty-one prey species were found: 13 species of gastropods, 4 bivalves, 12 crustaceans, and 2 echinoderms (Table 1). Some birds also contained remains of polychaets. A total of 8389 prey items were identified, of which 68.4% were gastropods, 18.5% were bivalves, and 13% were crustaceans (Table 1). In terms of aggregate wet weight, 31.4% was gastropods, 30.6% was bivalves and 38% was crustaceans (Table 1). The differences between frequency and weight proportions were due to large numbers of small gastropods (Fig. 2).

Gastropods.—Gastropods were found in 97% of the birds. *Margarites helicinus* and *Skeneopsis planorbis* made up 18.9% and 53.6%, respectively, of the total gastropod numbers (Table 1). However, 99.1% (n = 3047) of the *S. planorbis* were found in adult male eiders, one bird contained 2700 individuals (87.8%). The mean percentage by weight of gastropods in adults was 40.5 ± 8.1 (SE)%, while for juveniles it was 21.6 ± 8.3% (Fig. 2). *Margarites helicinus* and *Lacuna vincta* made up the largest proportions of the diet by mass in both juveniles (3.6 ± 1.1% and 12.2 ± 8.2%, respectively) and adults (15.6 ± 6.0% and 12.7 ± 4.0%, respectively). There

TABLE 1. Esophageal content of 29 Steller's Eiders collected in Varangerfjord, northern Norway, November 1996 to April 1997.

Taxa	No. of specimens (%)	Mean ± SE frequency	% of total wet weight	Mean ± SE wet weight	No. of birds (%)
Gastropoda					
Littorina saxatilis	30 (0.36)	1.30 ± 0.88	0.93	2.39 ± 2.34	5 (17.24)
L. obtusata	139 (1.66)	0.61 ± 0.26	2.03	1.14 ± 0.76	8 (27.59)
Thais lapillus	2 (0.02)	0.19 ± 0.19	0.05	0.03 ± 0.03	1 (3.45)
Trophonopsis truncatus	3 (0.04)	0.25 ± 0.22	0.13	0.26 ± 0.22	3 (10.35)
Lacuna vincta[a]	667 (7.95)	11.87 ± 2.80	10.19	12.48 ± 4.03	20 (68.97)
L. neritodea[a]	136 (1.62)	1.02 ± 0.62	1.44	0.94 ± 0.76	6 (20.69)
Margarites helicinus[a]	1087 (12.96)	18.33 ± 4.24	11.37	10.65 ± 3.65	23 (79.31)
M. groenlandicus[a]	28 (0.33)	1.11 ± 0.75	1.12	1.90 ± 1.19	8 (27.59)
Rissoa spp.[a]	184 (2.19)	2.53 ± 0.75	0.61	0.42 ± 0.13	15 (51.72)
Onoba spp.[a]	355 (4.23)	2.22 ± 1.05	0.31	0.18 ± 0.07	10 (34.48)
Buccinum groenlandicum	3 (0.04)	0.07 ± 0.06	0.03	0.02 ± 0.01	2 (6.90)
Skeneopsis planorbis[a]	3074 (36.64)	5.51 ± 2.86	2.69	1.59 ± 1.42	12 (41.38)
Amacea testidunalis	11 (0.13)	0.22 ± 0.12	0.32	0.39 ± 0.21	5 (17.24)
Unidentified species	20 (0.24)	0.28 ± 0.16	0.24	0.27 ± 0.20	6 (20.69)
Total of Gastropoda	5739 (68.41)	45.53 ± 5.67	31.44	32.67 ± 6.02	28 (96.55)
Bivalvia					
Mytilus edulis[a]	750 (8.94)	13.86 ± 4.10	27.02	21.00 ± 5.91	20 (68.96)
Tutornia minuta[a]	782 (9.32)	2.17 ± 1.07	1.26	0.64 ± 0.46	12 (41.38)
Musculus discors	10 (0.12)	0.05 ± 0.02	0.28	0.13 ± 0.12	5 (17.24)
Hiatella arctica	1 (0.01)	0.01 ± 0.01	—	—	1 (3.45)
Unidentified species	11 (0.13)	0.08 ± 0.04	2.02	0.81 ± 0.44	5 (15.63)
Total of Bivalva	1554 (18.52)	16.16 ± 4.26	30.59	22.58 ± 6.03	25 (86.20)
Polyplacophora spp.	1 (0.01)	—	—	—	1 (3.45)
Crustacea					
Isopoda					
Jaera spp.	51 (0.61)	1.84 ± 1.83	—	—	2 (6.90)
Idotea pelagica[a]	3 (0.04)	0.13 ± 0.13	—	—	1 (3.45)
I. emarginata[a]	169 (2.01)	5.61 ± 3.86	—	—	3 (10.35)
I. granulosa[a]	100 (1.19)	3.44 ± 2.80	—	—	8 (25.00)
I. baltica[a]	11 (0.13)	0.12 ± 0.12	—	—	2 (6.90)
Unidentified species	54 (0.64)	2.03 ± 1.16	—	—	4 (13.79)
Total of Isopoda	388 (4.63)	13.19 ± 5.55	14.42	14.50 ± 5.40	12 (41.38)
Amphipoda					
Gammarus oceanicus	212 (2.53)	13.10 ± 4.94	—	—	13 (44.83)
Gammarellus homari	5 (0.06)	0.18 ± 0.11	—	—	5 (17.24)
Amphithoe rubricata[a]	327 (3.90)	5.04 ± 1.87	—	—	12 (41.38)
Anonyx sarsi	8 (0.10)	0.21 ± 0.12	—	—	4 (13.79)
Calliopius laeviusculus[a]	14 (0.17)	0.56 ± 0.37	—	—	4 (13.79)
Onisimus edwortsi	1 (0.01)	0.03 ± 0.03	—	—	1 (3.45)
Caprella spp.[a]	67 (0.80)	3.31 ± 2.75	—	—	6 (20.69)
Unidentified species	70 (0.84)	1.30 ± 0.77	—	—	6 (20.69)
Total of Amphipods	704 (8.39)	24.40 ± 5.42	14.53	18.64 ± 5.76	23 (79.31)
Total of Crustacea	1092 (13.01)	37.59 ± 6.56	37.97	41.46 ± 7.38	24 (82.75)
Polychaeta	—	—	—	—	3 (10.34)
Echinodermata					
Stronglyocentrotus droebachiensis	1 (0.01)	—	—	—	1 (3.45)
Ophiopholis aculata	1 (0.01)	—	—	—	1 (3.45)

[a] Species commonly found on kelp plants (After Christie 1995, Norderhaug 1998).

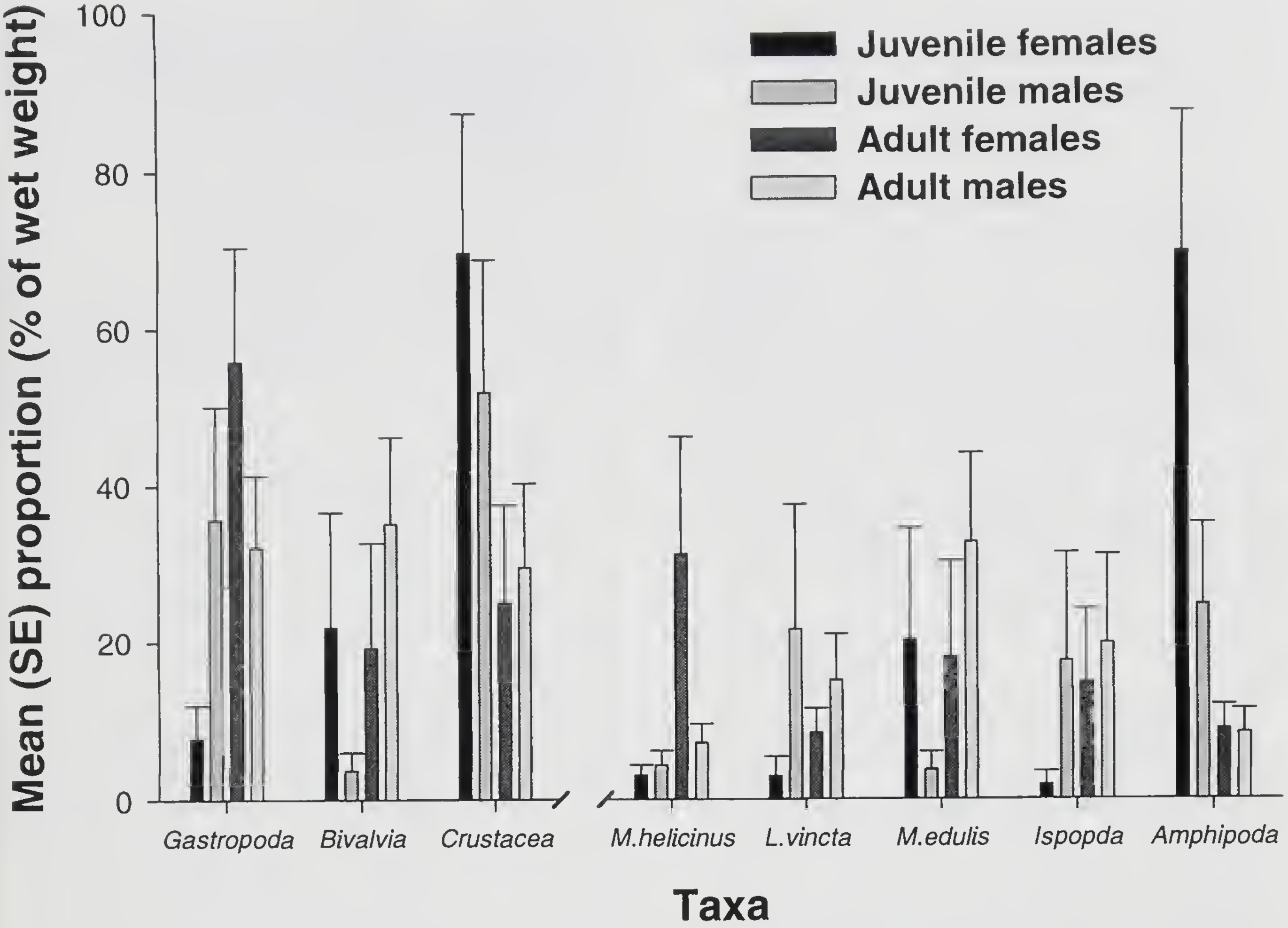

FIG. 2. The proportion (mean ± SE) of various prey types of Steller's Eiders, collected in Varangerfjord, northern Norway, November 1996 to April 1998.

was a significant interaction in the model between age and sex for proportion of aggregate wet weight consisting of gastropods ($F_{1,25} = 5.03$, $P < 0.05$), consequently we analyzed the sexes separately. Adult females ate significantly more snails than did juvenile females ($F_{1,11} = 10.01$, $P = 0.01$) but no such differences were found among adult and juvenile males ($F_{1,17} = 0.05$, $P > 0.05$; Fig. 2).

Bivalves.—Eighty-six percent of the birds had eaten bivalves, and 1554 specimens were identified (Table 1). Of these 48.3% were *Mytilus edulis* and 50.3% were *Turtonia minuta.* However, 99% of the *T. minuta* were found in adult male eiders; two males contained 98.5% of the total. Bivalves made up 30.6% of the aggregate wet weight (Table 1), of which 88.3% was *M. edulis.* In adult eiders, bivalves made up 29.5 ± 8.6%, but in juveniles they made up 12.8 ± 7.6%. The mean weight proportion of *M. edulis* was 27.4 ± 8.5% in adults and 11.9 ± 7.3% in juveniles (Fig. 2). Neither sex ($F_{1,26} = 0.08$, $P > 0.05$) nor age ($F_{1,25} = 1.66$, $P > 0.05$) had significant effects on the aggregate weight proportions of *M. edulis* in the diet (Fig. 2).

Crustaceans.—Overall, 83% of the birds were found to have eaten crustaceans. Of 1092 crustaceans identified, 64.5% were amphipods and 35.5% were isopods (Table 1). The most numerous amphipods were *Gammarus oceanicus* (30.1%) and *Amphithoe rubricata* (46.5%), while *Idotea emarginata* (43.6%) and *I. granulosa* (25.8%) were the most common isopods (Table 1). Overall 38% of the aggregate weight consisted of crustaceans (Table 1), of which isopods made up 49.8% and amphipods 50.2%. The mean proportion of crustaceans in juveniles was 60.7 ± 12.0% including those not identified beyond the crustacean group. When excluding the unidentified group, 9.6 ± 7.0% were isopods and 33.0 ± 8.6% were amphipods. The proportion of crustaceans in adults was 27.9 ± 8.1% (18.0 ± 7.8% isopods and 8.5 ± 2.6% amphipods; Fig. 2). Age ($F_{1,26} = 5.5$, $P =$

0.027), but not sex ($F_{1,26} = 0.50$, $P > 0.05$) had a significant effect on the proportion aggregate wet weight of crustaceans.

DISCUSSION

In terms of biomass, gastropods, bivalves, and crustaceans made up nearly equal proportions (30–40%) of the Steller's Eider winter diet. The prey species that were of particular importance (Table 1) are all common species in hard bottom communities, especially kelp beds, along the Norwegian coast (Christie 1995, Skadsheim and Rinde 1995, Norderhaug 1998). Metzner (1993) studied wintering Steller's Eiders in Izembek Lagoon in Alaska and found that 15% of the diet consisted of gastropods, 29% bivalves, and 30% crustaceans, indicating a similar diet as the Steller's Eiders in Varangerfjord. Petersen (1980, 1981) showed that *M. edulis* and the amphipod *Anisogammarus pugettensis* made up the majority (about 40% each) of the diet of molting Steller's Eiders in Nelson Lagoon, Alaska. In our study *M. edulis* was the species of which the birds ate the largest biomass (27%), probably a result of the ubiquitous nature of *M. edulis* (Seed 1976) and its availability in the study area. Steller's Eiders appear to have a higher proportion of amphipods and isopods in their diet than most other sea ducks (Cottam 1939; Madsen 1954; Johnsgaard 1975; Palmer 1976; Petersen 1980, 1981; Metzner 1993). This suggests that the Steller's Eider specializes in catching mobile prey. Moreover, because crustaceans have a much larger energy density per gram than shelled prey (Goudie and Ankney 1986, Guillemette et al. 1992), the high proportion of crustaceans eaten by Steller's Eiders suggests that the species has high energetic requirements. Larger sea ducks such as other eiders (*Somateria* spp.) and scoters (*Melanitta* spp.) usually feed on larger prey with lower energy content, mainly bivalves and echinoderms (Cottam 1939; Madsen 1954; Palmer 1976; Goudie and Ankney 1986; Bustnes and Erikstad 1988, 1990; Guillemette et al. 1992). The only other small-bodied sea ducks in northern Norway, the Oldsquaw (*Clangula hyemalis*), may also eat large proportions of isopods and amphipods. Generally they have a more diverse diet, including fish and fish roe, than the Steller's Eider (Cottam 1939; Madsen 1954; Sanger and Jones 1984; Johnson 1984; Goudie and Ankney 1986; Bustnes and Systad, unpubl. data).

The reason juveniles ate more crustaceans than adults (means of 60% vs 25%), might be that the former were in poorer body condition (Bustnes and Systad, unpubl. data) and needed more energy to survive. Foraging where the risk of starvation is minimized is often referred to as 'risk prone' foraging (Krebs and Kaclenik 1991) and may increase the survival probability if the expected energy budget is negative. Mean intake rate from a predictable food source may not result in a positive energy budget, but high returns from a variable source might. If the expected energy budget is positive, animals may benefit from selecting the least variable food source and be 'risk adverse' (see Krebs and Kaclenik 1991 for a review). While mollusks and bivalves are more or less stationary, crustaceans are mobile, probably making them less predictable prey. Birds in good condition may feed safely on predictable food sources with lower energy content, while birds in poor condition, such as juveniles, may need food with high energy density to survive (Guillemette et al. 1992).

In Varangerfjord the Steller's Eiders predominantly feed in areas with underwater vegetation, especially in kelp forest dominated by *Laminaria hyperborea* (Bustnes and Systad, unpubl. data). Such kelp beds are known to have a high diversity and biomass of potential prey for sea ducks. Recent studies have documented the distribution of invertebrates on the kelp plants along the Norwegian coast (Christie 1995, Skadheim and Rinde 1995, Norderhaug 1998). By comparing the species assemblages in kelp forest to the diet of Steller's Eider in Varangerfjord we found that more than 90% of the prey items were of species that commonly inhabit kelp plants (Table 1; Christie 1995, Norderhaug 1998). This strongly suggests that the vegetation itself is an important feeding habitat for this species. A similar conclusion may be drawn from a study in Izembek Lagoon, Alaska (Metzner 1993) where Steller's Eiders predominantly fed among eel grass (*Zostera marina*).

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ASSESSING THE EFFECTIVENESS OF PREDATOR EXCLOSURES FOR PLOVERS

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ABSTRACT.—We identified causes of nest failure and assessed the effectiveness of predator exclosures at Piping Plover (*Charadrius melodus*), Snowy Plover (*C. alexandrinus*), and Killdeer (*C. vociferus*) nests in southeastern Colorado during 1994–1995. Predation, nest abandonment, and weather were the primary causes of nest failure in all three species. For any of the three species we found no significant difference in the daily survival rate between nests that were protected by predator exclosures and nests that were unprotected. We reevaluated the experimental design and data analysis of previous predator exclosure studies and identified several confounding factors, including non-random assignment of exclosures, unbalanced sample sizes between protected and unprotected nests, data pooling across years, and inappropriate statistical analyses. We suggest ways to design (e.g., randomly allocate exclosures to nests and balance sample sizes between protected and unprotected nests) and analyze (e.g., use Mayfield method) future predator exclosure studies. *Received 25 May 1999, accepted 19 Oct. 1999.*

Conservation of endangered species requires a thorough knowledge of factors affecting their reproductive success and their survival during migration and winter. The Piping Plover (*Charadrius melodus*) and Snowy Plover (*C. alexandrinus*) are U.S. federally listed species throughout all or part of their ranges, respectively, in North America (U.S. Fish and Wildlife Service 1985, 1993, 1994b). Several factors may act to reduce Piping Plover and Snowy Plover reproductive success, including weather (Grover and Knopf 1982, Haig and Oring 1988, Sidle et al. 1992), nest abandonment (Cairns 1982, Grover and Knopf 1982, Warriner et al. 1986), and nest predation (Wilcox 1959, Grover and Knopf 1982, Page et al. 1983, Gaines and Ryan 1988, Haig and Oring 1988, Mayer and Ryan 1991, Paton 1995). Nest predation is considered a pervasive problem throughout the range of the Piping Plover (U.S. Fish and Wildlife Service 1994a, 1996) and has been documented as a primary threat to Snowy Plovers on their breeding grounds in California (Page et al. 1983) and Utah (Paton 1995).

One common technique used to reduce nest predation on shorebirds is to place predator exclosures around nests. Wire mesh predator exclosures have been used to protect Piping Plover nests on the Atlantic Coast, Great Lakes, and in the northern Great Plains (Rimmer and Deblinger 1990, Powell and Cuthbert 1992, Melvin et al. 1992) and Snowy Plover nests in California and Oregon (Page et al. 1995). Use of predator exclosures to reduce nest failure was a logical approach because nests could be protected from the primary nest predators including red foxes (*Vulpes vulpes*), striped skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*), gulls (*Larus* spp.), and crows (*Corvus* spp.).

To determine whether predator exclosures are an effective management tool to increase productivity throughout the breeding range of Piping Plovers and Snowy Plovers, however, it is necessary first to identify which predators are causing nest failure at each breeding location. It is critical to use an appropriate experimental design and we extend previous work in this area by conducting field experiments to assess exclosure effectiveness. A valid experimental design can compensate for small sample sizes (e.g., balanced sample sizes provide greater power) that are typical of endangered species research and is essential to draw accurate conclusions regarding exclosure effectiveness.

We focused our study on the Piping Plover and Snowy Plover because of their declining status, and included the Killdeer (*C. vociferus*) as a reference species because it is common

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and its breeding habitat overlaps that of the other two species. All are ground nesting shorebirds that incubate 2–4 eggs for about 26–28 d (Haig 1992, Warriner et al. 1986, Powers 1978). We tested the null hypothesis that there were no differences in daily survival rates of protected and unprotected nests of each species, and *a priori* predicted that nests protected by exclosures would have a higher daily survival rate than unprotected nests. Our objectives were to (1) evaluate the effectiveness of predator exclosures for Piping Plovers, Snowy Plovers, and Killdeers in Colorado; (2) determine the causes of nest failure for these species; and (3) examine the experimental design and analysis of previous predator exclosure studies of plovers.

STUDY AREA AND METHODS

We placed predator exclosures over 9 Piping Plover, 27 Snowy Plover, and 16 Killdeer nests in southeastern Colorado from 20 May to 7 August 1994, and over 28 Snowy Plover nests from 19 April to 12 August 1995. Our study sites included shorelines of John Martin Reservoir (Bent County) and altered and unaltered playa lakes throughout Kiowa and Prowers counties. All locations were characterized by open sandy beaches or alkaline flats. Water levels in all water bodies varied markedly between years because of intense spring rains and above normal mountain snow pack in 1995.

Nest searching, marking, and monitoring.—We located nests by surveying shorelines of playa lakes from a small boat or by walking along the shoreline and scanning for adults with a spotting scope. We marked nest sites with small wooden garden stakes protruding 5–8 cm above ground and placed at least 10 m from the nest. We referenced nest site markers with a compass bearing and distance to an inconspicuous object at least 50 m from the nest site. We visited nests every 3–4 d and recorded the number of eggs and the presence of any predator tracks from at least 10 m away to minimize the effect of our presence at the nest. During 1995, we floated eggs twice during incubation to predict hatching date (Hill 1985, Alberico 1995).

Predator exclosures.—Upon finding the first nest of each species at each study site, we randomly decided whether to apply a predator exclosure by flipping a coin. Thereafter, we alternated between applying the treatment (exclosure) or leaving the nest as a control (no exclosure) at subsequent nests. This procedure balanced the sample size between control and treatment nests as much as possible.

We designed exclosures to exclude large avian predators and medium to large mammalian predators. Exclosures were not designed to prevent entry of small mammalian or reptilian predators because this would have prohibited access to the nest by the incubating bird. We based exclosure construction on designs developed previously for shorebirds (Nol and Brooks 1982, Rimmer and Deblinger 1990, Deblinger et al. 1992, Melvin et al. 1992, Estelle et al. 1996) but smaller than those recommended for Piping Plovers on the Atlantic Coast. We constructed cylindrical exclosures 61 cm high and 112 cm diameter, from 16 gauge, 5 × 5 cm wire mesh for Piping Plovers and Snowy Plovers, and 14 gauge, 5 × 10 cm wire mesh for Killdeers. We covered the top of the exclosures with the same wire mesh materials used for each species. We wove four pieces of steel rebar (1.3 × 91 cm) through the sides of each exclosure to secure it to the ground, buried the bottom 10 cm of the exclosure in the ground, and secured it with four 15–20 cm tent stakes. We installed exclosures within 1 day of locating a nest and measured the installation time and the time it took a bird to return to the nest and resume incubation (return time).

Nest fate.—We classified a nest as successful when we observed at least one chick in or near a scrape or when we found an eggshell top or bottom indicative of a hatched egg (Mabee 1997). We classified a nest as failed when (1) a clutch of eggs disappeared too early in incubation to have hatched, (2) the nest area contained indications of predation (e.g., broken eggs and/or predator tracks at a nest), or (3) the clutch was abandoned. If we suspected a clutch was abandoned (i.e., no adult observed incubating the eggs or present in the area), we reoriented the eggs in the scrape. If egg orientation had not changed and there was not an adult present in the area on the subsequent nest check (i.e., 3–4 d later), we considered the clutch to have been abandoned. We classified a nest as having an unknown fate when we could not determine nest fate.

Nest failure.—We used a combination of techniques to identify potential nest predators. First, when a nest became inactive (either hatched or failed), we searched at least a 10 m radius around a nest for predator tracks or eggshells. We inspected eggshells with a 10× lens for sign of tooth or beak marks. We identified large mammalian predators and occasionally snakes by the presence of tracks at a nest site (Murie 1982, Brown and Morgan 1983, Halfpenny 1986). We identified avian predators by the characteristics of eaten eggshells (Rearden 1951, Anderson 1971) or presence of tracks and/or pellets at a nest site. When a clutch failed inside an exclosure, we inferred predation by rodents if eggshells were found at or near the nest or by snakes if no eggshells were found. We made these assumptions because the 5 × 5 cm mesh of exclosures precluded most other possible predators from reaching the nest. We classified the cause of nest failure as unknown predation when eggs were missing from an unprotected nest, were too early in incubation to have hatched, and there was no distinctive predator sign.

We placed a mammal tracking tube near each nest in 1995 to determine the presence of rodents occurring in nesting habitat. Tracking tubes consisted of PVC pipe 5 cm in diameter and 31 cm in length with a removable liner (Mabee 1998). We placed tracking tubes in comparable nesting habitat an average of 30

TABLE 1. Daily survival rates (DSR) of nests protected with predator exclosures and unprotected nests of Piping Plovers, Snowy Plovers, and Killdeers in southeastern Colorado, 1994–1995. Z values calculated following Johnson (1979).

Species	Protected nests DSR ± SE (n)	Unprotected nests DSR ± SE (n)	Z (P)
1994			
Piping Plover	0.976 ± 0.017 (5)	0.988 ± 0.012 (4)	−0.43 (>0.10)
Snowy Plover	0.984 ± 0.009 (13)	0.983 ± 0.008 (14)	0.05 (>0.10)
Killdeer	0.966 ± 0.017 (7)	0.994 ± 0.006 (9)	−1.24 (>0.10)
1995			
Snowy Plover	0.977 ± 0.009 (14)	0.973 ± 0.011 (14)	0.20 (>0.10)

m away from nests so as to not attract small mammals to the nests. We developed a reference collection of tracks from small mammals trapped with Sherman traps at each of the study locations.

We classified clutches as abandoned when the complete clutch was abandoned and the eggs were fertile. Clutches that lost eggs to predators or cattle trampling and subsequently deserted were not classified as abandoned because the cause of failure could have been events preceding the nest abandonment.

Statistical analysis.—We calculated a daily survival rate for protected and unprotected nests for each species using the Mayfield method (Mayfield 1961, 1975) because it correctly weights the importance of successful, failed, or unknown fate nests by basing the daily survival rate on the number of nest exposure days. We calculated standard errors and tested for differences in daily survival rates between protected and unprotected nests with a Z test (Johnson 1979) and $\alpha = 0.10$. We selected this α level *a priori* because we expected small sample sizes and wanted to reduce the risk of a type II error. We also calculated observed nest success (successful nests/total nests) to facilitate comparison between studies that protected individual nests with predator exclosures and those that did not.

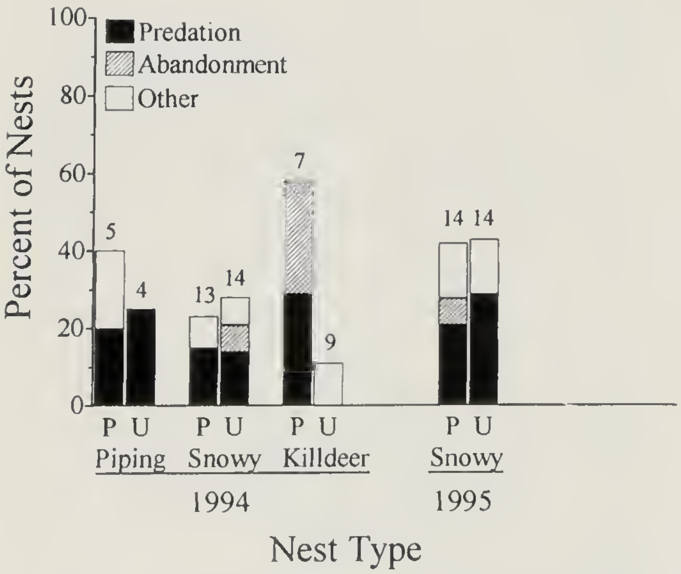

FIG. 1. Percent of protected (P) and unprotected (U) nests of Piping Plover (Piping), Snowy Plover (Snowy), and Killdeer that failed because of predation, abandonment, and other causes in southeastern Colorado, 1994–1995. Numbers above bars indicate sample size for each bar.

RESULTS

Effectiveness of predator exclosures.—Mean exclosure installation times (± SE) were similar among Piping Plover (13.0 min ± 1.3), Snowy Plover (12.2 ± 0.8), and Killdeer nests (9.5 ± 1.8) in 1994, and also for Snowy Plover nests (10.4 ± 0.7) in 1995. Average return times were similar for Piping Plovers in 1994 (6.0 ± 3.2) and Snowy Plovers in 1994 (6.1 ± 1.5) and 1995 (4.0 ± 1.1) but not for Killdeers in 1994 (25.0 ± 9.0). Because we collected return times opportunistically, we did not conduct statistical tests for differences among species.

We found no significant difference in the daily survival rate between protected and unprotected nests of Piping Plover ($n = 5$ protected, 4 unprotected), Snowy Plover ($n = 13$, 14), or Killdeer ($n = 7$, 9) in 1994 or Snowy Plover ($n = 14$, 14) in 1995 ($P > 0.10$ for all cases; Table 1).

Causes of nest failure.—No single predator or abiotic factor was responsible for most nest failure of the three species. Predation was the primary cause of nest failure during both years, whereas abandonment varied in importance by year (Fig. 1). Causes of nest failure classified as other included nest losses caused by cattle trampling, human disturbance or removal of eggs, beetles burrowing through eggs, sterile eggs, and partial clutch loss followed by abandonment. In 1994, protected nests were depredated by small predators, including snakes ($n = 1$), snake or Great Plains

TABLE 2. Observed nest success (number hatched/total nests) for nests protected with individual predator exclosures and unprotected nests of Piping Plovers, Snowy Plovers, and Killdeers in North America.

Species	Protected nests % (*n*)	Unprotected nests % (*n*)	Author
Piping Plover	92 (26)	25 (24)	Rimmer and Deblinger 1990
	90 (29)	17 (24)	Melvin et al. 1992
	60 (5)	75 (4)	This study 1994
	—[a]	0 (8)	This study 1995
	—	91 (4)	Wilcox 1959
	—	76 (51)	Cairns 1982
	—	36 (72)	Haig and Oring 1988
	—	35 (49)	MacIvor et al. 1990
Snowy Plover	69 (13)	57 (14)	This study 1994
	57 (14)	54 (13)	This study 1995
	—	53 (2123)	Page et al. 1995
Killdeer	33 (12)	29 (17)	Nol and Brooks 1982
	14 (7)	33 (9)	This study 1994
	—	24 (41)	This study 1995

[a] — No data.

skink (*Eumeces obsoletus*; *n* = 1), snakes or rodents (*n* = 3), and 2 clutches were sterile. In 1995, losses were caused by rodents (*n* = 2), snake or rodent (*n* = 1), sterile eggs (*n* = 1), and partial clutch loss by an unknown predator followed by abandonment (*n* = 1). Of all tracks identified at tracking stations placed in nesting habitat of all species in 1995, 99% were from deer mice (*Peromyscus maniculatus*), with the remaining tracks from northern grasshopper mice (*Onychomys leucogaster*) and an unidentified rodent. No large predators caused nest failure at protected nests in either year.

Unprotected nests in the exclosure experiment in 1994 failed because of Great Blue Heron (*Ardea herodias*) predation (*n* = 1), unknown predators (*n* = 2), a suspected burrowing beetle (*Geospinus* sp.) that burrowed through eggs (*n* = 1), and cattle trampling (*n* = 1); in 1995 unprotected nests failed because of unknown predators (*n* = 4), cattle trampling (*n* = 1), and partial clutch loss by cattle trampling followed by abandonment (*n* = 1).

DISCUSSION

Nest failure.—Although exclosures were exposed to predators of various sizes [e.g., coyotes (*Canis latrans*) to snakes], the protected nests appeared vulnerable only to reptilian or small mammalian predators. We observed bullsnakes (*Pituophis melanoleucus*) and coachwhips (*Masticophis flagellum*) commonly on the prairie and detected deer mice at all study sites. Deer mice were documented to eat or destroy eggs of nesting Spotted Sandpipers (*Actitis macularia*; Maxson and Oring 1978).

Unprotected nests were vulnerable to all predators, and this made it difficult to attribute predation to a specific species. We attributed 25 of 41 depredated nests to unidentified predators and no single identified predator species caused a majority of nest failure of the remaining nests. Early season plover nests were also vulnerable to tornadoes, hail storms, and flooding in 1995 that resulted in crushed eggs, inundated nests, and dead Killdeer chicks. Nest abandonment rates we observed fell within the range of values reported in other plover studies (Vaske et al. 1994). For comparative purposes, we examined the observed nest success of various plover studies. During 1994, the observed nest success for unprotected nests of Piping Plovers in our study area was higher than the average value from protected and unprotected nests found in other predator exclosure studies, whereas it was intermediate compared to several other non-exclosure studies (Table 2). During both years of this study, the average observed nest success for unprotected nests of Snowy Plovers was comparable to the average value obtained from non-exclosure studies throughout the breeding range (Table 2).

Predator exclosure study.—Our exclosures worked well structurally (no large avian or mammalian predators reached protected nests) and did not affect incubating behavior (all species entered and exited exclosures with ease). Ultimately, however, our exclosures did not increase the daily survival rates for Snowy Plover nests and the same appears to be true for Piping Plover and Killdeer nests. Although the small sample sizes may have diminished our ability to detect differences in the daily survival rate of Piping Plover and Killdeer nests in 1994, the results obtained from these species were consistent with those obtained from the larger sample of Snowy Plover nests in both years. Because Piping Plovers and Snowy Plovers are similar in several ways (behavior, nesting habitat, exposure to predators, causes of nest failure), we might expect exclosure effectiveness to be comparable for these species. Killdeers behaved differently, perhaps making them more susceptible to nest abandonment for protected nests and therefore require further study to assess the utility of exclosures.

The results of our predator exclosure study (especially for Snowy Plovers) stand in contrast to the results of studies that reported increased nest success associated with nest exclosures [Rimmer and Deblinger 1990 (χ^2 = 20.84, 1 df, $P < 0.001$), Melvin et al. 1992 (χ^2 = 26.64, 1 df, $P < 0.001$)]. We believe the main differences are due to different predator communities (i.e., most predation is from medium-sized birds and mammals on the Atlantic Coast in contrast to small animals in Colorado) and predation intensity (higher rates of predation on Atlantic Coast nests) and secondarily because of differences in experimental design. We examined the experimental design and analyses in other studies and determined that they assigned exclosures nonrandomly to nests, had unbalanced sample sizes of protected and unprotected nests both within and between years, pooled data across years, and used observed nest success (Rimmer and Deblinger 1990) as the metric to compare the effectiveness of exclosures. In contrast, Nol and Brooks (1982) and our study randomly allocated exclosures to nests, had nearly balanced sample sizes between protected and unprotected nests, did not pool data across years, and compared exclosure effectiveness with estimates based on the Mayfield method (Mayfield 1961, 1975).

Random assignment of exclosures to nests is essential to determine the degree of exclosure effectiveness because it controls for confounding factors such as investigator bias, stage of incubation, location, microhabitat, and time of season. In two studies, non-random treatment assignment resulted in artificially decreased rates of nest success for unprotected nests. This occurred because nests at which exclosures were not accepted, that failed during egg laying (Melvin et al. 1992), that were already destroyed when found, or that failed before exclosures could be applied, were classified as unprotected (control) nests (Rimmer and Deblinger 1990). Unbalanced treatment assignment leads to decreased power in statistical tests whereas data pooling across years can provide biased results.

The type of analysis used to determine the magnitude of a treatment effect is also important. For example, we used data from Nol and Brooks (1982) and found no significant difference in the observed rate of nest success between protected and unprotected nests using Fisher's exact test ($P = 0.737$), consistent with the authors' finding of no significant difference in overall rates of nest predation between protected and unprotected nests. However, this finding stands in contrast to the significant difference in daily survival rate between protected (0.963) and unprotected (0.951) nests that we calculated using the Mayfield method ($P < 0.001$). In another example, Rimmer and Deblinger (1990) and Melvin and coworkers (1992) compared the effectiveness of exclosures by using observed nest success data and the daily survival rate, respectively with χ^2 tests. Because daily survival rates are a proportion, they are not suitable for a χ^2 test (Zar 1998) but should be compared with a Z test (Johnson 1979). Observed nest success can overestimate actual nest success (Mayfield 1961, 1975) and hence may inflate exclosure effectiveness.

The primary objectives in the predator exclosure studies of Rimmer and Deblinger (1990) and Melvin and coworkers (1992) were to protect most of the Piping Plover nests, and the effectiveness of exclosures was analyzed retrospectively. This fundamental difference between their study objectives and ours created many of the differences that we have noted. We believe that exclosures increased nest success in both the Rimmer and Deblinger (1990) and Melvin and coworkers (1992) studies, although we may not be able to calculate the degree of exclosure effectiveness accurately.

To protect declining species such as Piping Plover and Snowy Plover on breeding grounds, we recommend that researchers (1) identify the causes of nest failure, (2) select an appropriate management tool (e.g., predator exclosures), (3) use a rigorous study design and analysis (e.g., Mayfield method) in order to test the effectiveness of exclosures, and (4) decide if predator exclosures are the most effective use of limited time and resources. We recommend that exclosures should not be used on Snowy Plovers in southeastern Colorado as long as small animal predators (e.g., reptiles and rodents) are the dominant causes of nest failure. Instead, we recommend increased protection of shorelines from disturbances caused by human activities and cattle grazing. Although it is likely that Piping Plovers will experience similar rates and causes of nest predation as Snowy Plovers in Colorado, additional study is needed for this species. Continued nest monitoring is needed for both species to ensure appropriate management recommendations in the future.

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HOME RANGE CHARACTERISTICS OF MALE COOPER'S HAWKS IN AN URBAN ENVIRONMENT

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ABSTRACT.—We monitored the movements of nine radio-tagged, adult, male Cooper's Hawks (*Accipiter cooperii*) in adjacent home ranges during the breeding seasons of 1996 or 1997 in Tucson, Arizona, to ascertain the sizes and degree of overlap of home ranges, and to assess habitat selection at two spatial scales. Size of home ranges differed among hawks (13.3–130.6 ha), but the average was small [65.5 ha ± 40.7 (SD)] compared to the size of home ranges reported for Cooper's Hawks in the literature. Home range size generally decreased with the number of years that a hawk had lived on its breeding territory. Only one pair of home ranges overlapped each other; overlap of one home range on the other in this pair was 14.2% and 10.6%. Proportions of land-use categories in home ranges varied widely among hawks, and suggested that the hawks did not select their home ranges on the basis of the categories we examined. Patterns of habitat use inside individual home ranges suggested that male hawks hunted primarily in the environments that surrounded their nests. Cooper's Hawks in Tucson feed primarily on doves [Mourning Doves (*Zenaida macroura*), Inca Doves (*Columbina inca*), and White-winged Doves (*Zenaida asiatica*)], and we speculate that the abundance of doves throughout Tucson allowed the hawks to hunt successfully in several urban environments. We also speculate that Cooper's Hawks in Tucson have relatively small home ranges because they do not need to range far from their nests to find food.
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Cooper's Hawks (*Accipiter cooperii*) generally nest in undeveloped forests and woodlands (Reynolds 1989, Rosenfield and Bielefeldt 1993), but they occasionally nest in towns and cities (Stahlecker and Beach 1979, Murphy et al. 1988, Rosenfield et al. 1995, Stewart et al. 1996, Boal and Mannan 1998). Reported densities of nesting Cooper's Hawks in undeveloped environments range from 1 nest every 671–2326 ha in the western United States (Reynolds 1989), and from 1 nest every 331–5000 ha in the eastern United States (Rosenfield et al. 1991). Estimates of nest density in some urban/suburban environments are among the highest reported. For example, Rosenfield and coworkers (1995) found a density of 1 nest every 272 ha for Cooper's Hawks in Stevens Point, Wisconsin, and Boal and Mannan (1998) found an overall density of 1 nest every 437 ha in Tucson, Arizona.

The density of nests in an area is determined largely by the density and quality of resources required for breeding (e.g., nest sites, food), with the upper limit being set by spacing behavior in territorial birds (Newton 1986). As the conditions that promote a high density of nests become more prevalent in an area, the size of individual home ranges and the amount of overlap among neighboring home ranges might change in one of two ways. First, the average size of home ranges could decrease, and overlap of neighboring home ranges might, therefore, remain about the same. Conversely, if the size of home ranges remains stable as nest density increases, overlap among neighboring home ranges might increase. It is also possible that home range size and overlap could fluctuate among different stages of the annual cycle (Newton 1986). We monitored the movements of male Cooper's Hawks during the breeding season in an urban environment where nest density was relatively high (1 nest every 362 ha) to ascertain the sizes and degree of overlap of home ranges. Because density of nests is determined in part by quality of resources, and habitat quality may vary among urban environments, we also looked for evidence of habitat selection by male Cooper's Hawks. We investigated habitat selection by assessing where Cooper's Hawks placed their home ranges relative to available urban environments (i.e., home range selection), and by assessing how Cooper's Hawks used different environments inside their home ranges (i.e., intra-home range selection; Johnson 1980).

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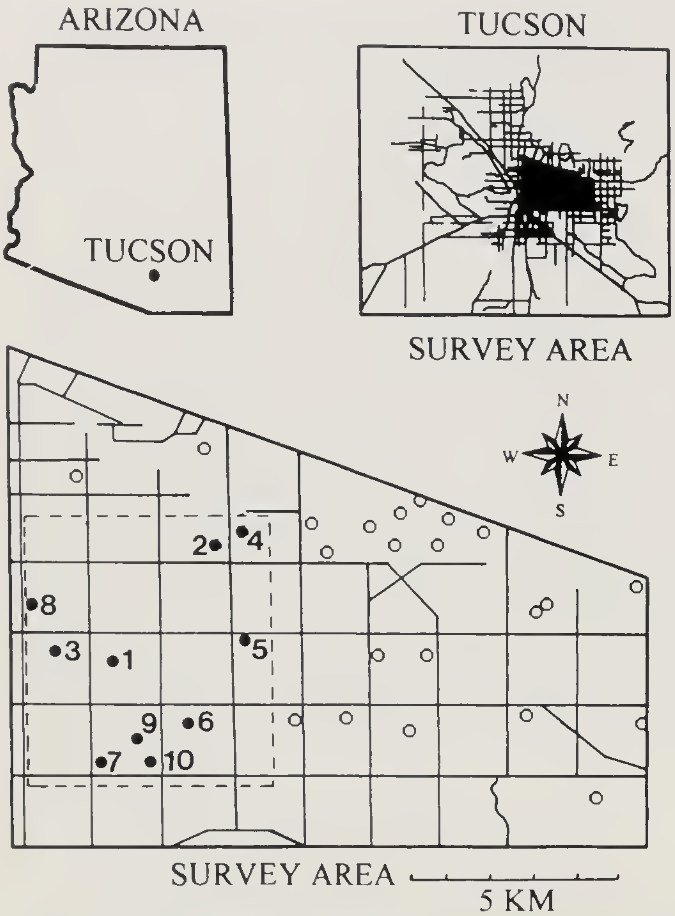

FIG. 1. Location of Tucson, Arizona (top left), the survey area within Tucson (top right, in black), and distribution of nests (● and ○) in the survey area in 1996 and/or 1997 (bottom). Solid circles indicate nests where males were captured and radio-tagged within the survey area (1 = Terra Alta, 2 = San Carlos, 3 = Himmel Park, 4 = Torino, 5 = Swanway Park, 6 = Cooper, 7 = Reid Park, 8 = Adams, 9 = Randolph North, 10 = Randolph South). The rectangular area (dashed line), which encompasses the home ranges of radio-tagged males, is 3618 ha.

STUDY AREA AND METHODS

Study area.—We studied Cooper's hawks in Tucson, Arizona (32° N, 111° W; Fig. 1). The Tucson metropolitan area encompasses approximately 70,000 ha and has a human population of about 800,000. Tucson is located in the Sonoran Desert and supports Lower and Upper Sonoran vegetation types and riparian corridors (Brown et al. 1979). Although remnants of these vegetative communities persist in Tucson, much of the natural vegetation has been removed or replaced with exotic plants.

The hawks we monitored occupied home ranges that were clustered in a 3618 ha area that was part of a larger area we had surveyed intensively for the presence of nesting Cooper's hawks (Boal and Mannan 1998; Fig. 1). Land in the area surveyed was used primarily for private residences, businesses, parks and golf courses.

Radio telemetry.—We monitored the movements of adult, male Cooper's Hawks in adjacent home ranges (Fig. 1) during the breeding seasons (March–July) of 1996 or 1997. We captured the hawks near their nests with dho gaza traps or bal-chatri traps (Bloom 1987) and attached a Holohill PD-2 transmitter (Holohill Systems, Ltd., Ontario, Canada) with a 6-month battery life to a tail feather of each hawk (Giroux et al. 1990). The transmitters weighed 3.5 g and were less than 2% of the body weight of males.

We relocated radio-tagged hawks with the homing technique (White and Garrott 1990) aided by Telonics (Telonics, Mesa, Arizona) TR-2 and TR-4 receivers with model RA-14 flexible, two-element yagi antennas. Cooper's Hawks in Tucson are acclimated to the presence of humans (Boal and Mannan 1999) and single observers could approach hawks without frightening them. Therefore, we attempted to see the hawks at each relocation. Sometimes hawks were out of sight (e.g., in a back yard), but they were close enough that their radio signal was detectable without an antenna. In such cases, the location of the hawk was estimated to be within 10 m of the point of the strongest signal. When the radio signal indicated a hawk was in a nest tree or nest grove, we stayed away from the nest and attempted to see the hawk with binoculars to reduce disturbance at the nest.

We relocated each radio-tagged hawk 5–10 times per week. We relocated hawks throughout the day and attempted to uniformly spread the relocations of each hawk among four periods (05:00–09:00, 09:00–13:00, 13:00–17:00, and 17:00–20:00 MST or darkness). Once the location of a hawk was determined, we mapped its position and recorded the general environment in which it was found (e.g., residential area, park, golf course). We stopped tracking a hawk after we recorded its location and did not relocate it again for at least 4 hours to minimize the risk of dependency between locations. We selected the 4 hour period based on the general rule that locations at times t_1 and t_2 can be considered statistically independent if the period between t_1 and t_2 is sufficient to allow the animal being followed to move from one end of its home range to another (White and Garrot 1990).

Seasonal patterns of movement for many animals correspond to biological cycles; thus, comparison of home ranges among different individuals must be done during the same periods of their cycles (Samuel and Fuller 1994). We chose to estimate home range size from early in the nesting cycle (i.e., nest building or incubation) until after the nestlings had fledged. We found that Cooper's Hawks in Tucson tended to make obvious deviations from their established home ranges about six weeks after their nestlings had fledged, probably coincident with fledglings approaching independence. The information we present is, therefore, from relocations taken from the day following tagging to six weeks post-fledging.

Analyses.—We transposed mapped locations of all hawks onto 7.5 minute series topographical maps, and then calculated Universal Transverse Mercator (UTM) coordinates and entered them into a database. We estimated size of home range for each hawk and overlap

TABLE 1. Size of home ranges (ha) for adult, male Cooper's Hawks during the breeding season in Tucson, Arizona, 1996 or 1997.

Nest	Period tracked	n[a]	100% MCP[b]	Adaptive kernal		Years of residency
				90%	95%	
Terra Alta	3/23–7/4/97	97	194.6	104.7	130.6	1
San Carlos	4/12–6/28/97	71	149.3	30.6	114.8	1
Himmel Park	3/16–7/17/96	102	132.9	43.2	88.7	1
Torino	5/24–6/29/97	60	66.1	38.9	85.2	1
Swanway Park	3/11–6/29/97	93	74.4	17.2	45.6	2
Cooper	2/27–6/28/97	88	115.1	3.3	41.4	≥2
Reid Park	6/11–8/8/96	30	39.5	34.7	39.9	2
Adams	5/13–7/20/96	43	23.1	25.5	29.8	2
Randolph North	3/23–6/28/97	73	20.9	6.9	13.3	≥4
Mean			90.7	33.9	65.5	
SD			60.8	29.9	40.7	

[a] Number of relocations for each hawk.

[b] Minimum Convex Polygon.

among home ranges within a given year with the adaptive kernel method (95% isopleth; Worton 1989). We generated area-observation curves (Odum and Kuenzler 1955) for each home range, based on the 95% isopleth, to evaluate whether our sample of relocations adequately described home range size for the period of interest. For purposes of comparison with past work, we also estimated the size of home range for each hawk with the 100% minimum convex polygon (MCP) method after discounting one obvious outlier for one bird. We used program RANGES V (Kenward and Hodder 1996) for all of the analyses related to home ranges.

We had color-marked breeding adults in the study area since 1994 (Boal 1997); thus, we knew the exact or minimum number of years that a male had occupied its home range. We examined the relationship between home range size (based on the 95% isopleth and the 100% MCP) and the number of years of residency with linear regression (Ramsey and Schafer 1997). We transformed size of home range (i.e., the response variable) with a log transformation because variability increased as the mean increased (Ramsey and Schafer 1997). Regression analyses were conducted in the JMP IN 3 Windows Version statistical package (SAS Institute Inc. 1996).

We overlaid the 95% isopleth for each home range onto a digital database coverage of land use categories in Tucson (Shaw et al. 1996). We queried the database for coverage of each category in each home range, compared the coverages with aerial photographs to assess accuracy, and corrected coverages in one home range. We then pooled the categories in all home ranges to generate a total estimate of the categories used by Cooper's Hawks (Thomas and Taylor 1990). The percentages of land use categories in each home range and in all home ranges combined were compared to the availability of the categories in a rectangular area that encompassed all home ranges (Thomas and Taylor 1990). These comparisons allowed us to examine habitat selection at the spatial scale of the home range (Johnson 1980). We also examined habitat selection by each hawk inside its home range by comparing the observed number of locations in each category to the number that would be expected if a hawk used each category in proportion to its occurrence within the home range. All comparisons of "use versus availability" ($n = 10$) were made with χ^2 Goodness-of-fit tests (Sokal and Rohlf 1995). We adjusted the level of alpha we considered significant for the Goodness-of-fit tests from 0.05 to 0.005 based on the Bonferroni adjustment (Sokal and Rohlf 1995). Goodness-of-fit tests were conducted in the Statistical Package for the Social Sciences (SPSS) Version 2 on MS Dosshell Version 2.78.

RESULTS

Home range size and overlap.—We radiotagged 10 male Cooper's Hawks during the study and obtained sufficient relocations on 9 of them to estimate home range size (Table 1). Relocations ($n = 657$) of all hawks were spread throughout the day (05:00–09:00: 27%; 09:00–13:00: 24%; 13:00–17:00: 21%; 17:00–dark: 27%). Most relocations (79% of 513) away from the nest tree/grove were based on visual sightings. All 9 home ranges were relatively stable in size throughout the breeding season, and none increased more than 5% over the last 10 locations (Fuller and Snow 1988). Mean size of home ranges, based on the 95% isopleth, was 65.5 ha (median = 45.6 ha; range = 13.3–130.6 ha; Table 1). However, 90% of the relocations occurred, on average, within 33.9 ha (median = 30.6; range = 3.3–104.7 ha; Table 1). Only one pair of

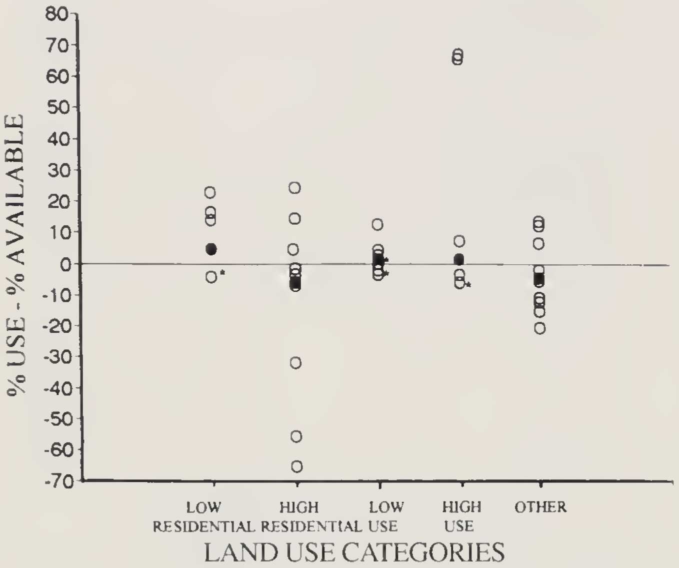

FIG. 2. Percent use minus percent available of land use categories in the home ranges of nine male Cooper's Hawks (○) and the total of all home ranges (●) in Tucson, Arizona, 1996–1997 (* indicates that more than one hawk is represented by a single ○). Percent available for each category was calculated from a rectangular 3618-ha area that encompassed all home ranges ($\chi^2 = 56.3$, 4 df, $P < 0.001$). Low Residential ≤ 7.6 residences per ha; High Residential ≥ 7.6 residences per ha; Low Use = cemeteries, neighborhood parks, and natural open space; High Use = golf courses, district and regional parks, and schools; Other = roadways, and commercial, agricultural, and industrial areas.

home ranges (San Carlos and Torino, Fig. 1) overlapped each other. The home range of the San Carlos male overlapped the home range of the Torino male by 14.2%, and the home range of the Torino male overlapped the home range of the San Carlos male by 10.6%. Size of home range, based on the adaptive kernal method (95% isopleth), decreased with the number of years that a male had occupied his territory [Table 1; linear regression: log of home range area = 2.28 − 0.31 × (years of residency); r^2 adjusted = 0.89; $F_{1,7} = 65.58$; $P < 0.001$]. The relationship between size of home range and years of residency was similar, but not as strong, when home range size was estimated with the MCP method [Table 1; linear regression: log of home range area = 2.33 − 0.27 × (years of residency); $r^2 = 0.51$; $F_{1,7} = 9.25$; $P = 0.019$].

Home range selection.—There was apparent selection by Cooper's Hawks for some land use categories when the combined home ranges of all nine hawks were compared to the area encompassing the home ranges (Fig. 2). For example, high density residential areas and commercial districts and roadways (i.e., "other") were present in the combined home ranges less than expected based on availability, and low density residential areas were present in the combined home ranges more than expected based on availability ($\chi^2 = 56.3$, 4 df, $P < 0.001$; Fig. 2). Percent of land use categories among individual home ranges, however, varied considerably (Fig. 2). Some home ranges were dominated by high density residential areas, whereas others were dominated by parks and golf courses (Table 2). No single land use category was consistently selected or avoided by all hawks when the composition of individual home ranges was compared to the composition of the area encompassing the home ranges (Fig. 2).

TABLE 2. Percentages of locations by land use categories[a] in home ranges of male Cooper's Hawks during the breeding season in Tucson, Arizona, 1996, 1997.

	Percent of locations (percent of home range)				
Nest	Low residential	High residential	Low use	High use	Other
Adams*[b]	0 (0)	100 (64.0)	0 (4.1)	0 (0)	0 (31.9)
Cooper*	0 (0)	100 (79.5)	0 (5.4)	0 (0)	0 (15.0)
Himmel Park*	0 (0)	13.4 (71.1)	0 (0.2)	86.6 (13.4)	0 (15.3)
Randolph North*	1.4 (19.9)	0 (0)	0 (6.0)	98.6 (74.2)	0 (0)
Reid Park*	0 (0)	0 (8.5)	0 (6.8)	100 (75.0)	0 (9.7)
San Carlos*	91.0 (27.0)	9.0 (58.2)	0 (7.0)	0 (1.3)	0 (6.5)
Swanway*	0 (0)	40.4 (62.1)	56.2 (10.4)	0 (0)	3.4 (27.5)
Terra Alta*	0 (0)	94.6 (89.7)	2.1 (0.2)	0 (0)	3.2 (10.1)
Torino*	1.8 (17.0)	78.6 (34.2)	19.6 (17.4)	0 (0)	0 (31.3)

[a] Low residential ≤7.6 residences per ha. High residential ≥7.6 residences per ha. Low use = cemeteries, neighborhood parks, and natural open space. High use = golf courses, district and regional parks, and schools. Other = roadways, and commercial, agricultural, and industrial areas.

[b] Asterisks denote that a significant difference ($P < 0.005$) was found between observed and expected frequencies of locations among land use categories (Goodness-of-fit test, Bonferroni correction). Categories with zero values were lumped to meet assumptions of the test.

Intra-home range selection.—Habitat selection inside individual home ranges also varied among hawks, but some patterns emerged. For example, all hawks avoided roadways, and commercial, agricultural and industrial areas (i.e., the "other" category) when they were present in their home ranges (Table 2). All but two hawks (Swanway and San Carlos) used either high density residential areas or regional parks and golf courses more than expected based on their availability (Table 2). The Swanway male predominantly used a small, neighborhood park and high density residential areas, and the San Carlos male used low density residential areas (Table 2).

DISCUSSION

Estimates of home range size for breeding Cooper's Hawks, based on nest density, range from 400 to 1800 ha (Craighead and Craighead 1956, Reynolds 1989). Estimates of home ranges during the breeding season, based on radio telemetry, vary from 784 ha for a male in a suburban area of Wisconsin (Murphy et al. 1988) to an average of 1206 ha for males in the Jemez Mountains of New Mexico (Kennedy 1989). The home ranges of male Cooper's Hawks in Tucson comparatively were small (65.5 ha).

Newton (1986) found that Sparrowhawks (*Accipiter nisus*) in Scotland became sedentary when prey animals were abundant and ranged widely when prey animals were scarce. We speculate that the abundance of prey in Tucson most likely accounts for the small home ranges we observed. Our speculation is supported by evidence that urban areas generally support a higher total density and biomass of birds than non-urban areas (e.g., in Tucson, Emlen 1974; elsewhere, Beissinger and Osborne 1982, Blair 1996, Marzluff et al. 1998). Furthermore, Mourning Doves (*Zenaida macroura*) and Inca Doves (*Columbina inca*) are the second and fourth most abundant birds in Tucson and their numbers are positively correlated with increasing housing density (Germaine et al. 1998). Doves also are abundant in parks and golf courses, and account for 84% of the identified prey (n = 121) at 45 Cooper's Hawks nests in Tucson (Boal 1997). We frequently observed prey captures and capture attempts in and near the nest tree and suggest that Cooper's Hawks do not need to range far from their nests to find food.

The home range sizes of Cooper's Hawks in Tucson, although relatively small, differed considerably among individuals. A variety of factors potentially influence home range size, including the abundance of prey, stage of the annual cycle, and age and sex of the hawk. Our data hint that there is a relationship between the size of home range and the number of years of residency. For example, all four of the largest home ranges (based on the adaptive kernal method, 95% isopleth), including the only two that overlapped, were occupied by new males. Lack of familiarity with their home ranges may have promoted more exploration by these males during hunting forays than males in more established home ranges. Increased efficiency in foraging with increasing age, especially in the first year of life, is common in birds (Wunderle 1991). Therefore, it seems reasonable to suggest that hawks, even as adults, become more efficient as they learn about a new area, and that this efficiency should increase most in the first year or two of residency.

Variation in the composition of individual home ranges when compared to the composition of the area that surrounded them suggests that male Cooper's Hawks in Tucson do not select home ranges on the basis of the land use categories we examined. Patterns of habitat use by Cooper's Hawks inside their home ranges also suggest that they are flexible in the types of urban environments they use. Within their home ranges, individual hawks usually were located more often than expected in either residential areas, regional parks and golf courses, or small, neighborhood parks. We speculate that because doves are abundant throughout Tucson (Germaine et al. 1998) individual preferences for where hawks spend their time, and thus where they likely hunt most frequently, may be influenced largely by location of the nest. Nests of Cooper's Hawks in Tucson usually are in groves of large, exotic trees [aleppo pine (*Pinus halepensis*) and *Eucalyptus* spp.] which are most common in older neighborhoods, city parks, golf courses, and cemeteries (Boal and Mannan 1998). Our findings contrast with the only other information about habitat selection by urban-dwelling Cooper's Hawks. Murphy and coworkers

(1988) found that the single male they tracked selected undeveloped woodlands and shrublands and avoided wooded residential areas and residential areas/businesses.

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AGE-SPECIFIC STOPOVER BEHAVIOR OF MIGRANT BALD EAGLES

MARCO RESTANI[1,2]

ABSTRACT.—A review of stopover behavior in birds revealed that most migrate as quickly as fuel reserves allowed (i.e., were time minimizers). This pattern stemmed from studies conducted almost exclusively on small-bodied species (< 50 g), which migrate primarily by flapping flight. However, body size has a significant effect on metabolic rate and costs of locomotion, two characteristics with direct relevance to migration and stopover behavior. I examined the autumn stopover behavior of a large-bodied species (4–5.5 kg) that migrates by soaring. I captured and radio-tagged 68 Bald Eagles (*Haliaeetus leucocephalus*) at Hauser Reservoir, Montana from 1992–1994. After capture, juveniles stayed at the stopover site longer than older eagles. Body condition was similar between the two age groups and did not correlate with post capture residence time. Consumption rates of eagles were not age-specific. Juvenile and 1.5-year old eagles had similar consumption rates and body condition, but differed in residence times, which suggested that experience modified stopover behavior. Stopover behavior of Bald Eagles supported the hypothesis that large species are less sensitive than small species to body condition and consumption rates during migration. *Received 29 April 1999, accepted 24 August 1999.*

During the journey between breeding and wintering grounds, migrating birds must make many important decisions: when to migrate, what route to take, and where to rest and feed (Gwinner 1977, Kerlinger 1989, Berthold and Terrill 1991). The behavior of birds at migratory stopovers, those places used for resting and replenishing depleted energy reserves, is of particular ecological interest because it is there that migrants must balance time and energy constraints, reconcile conflicting demands of foraging and predator avoidance, and evaluate weather conditions. Researchers find it difficult to determine how these factors affect stopover behavior because they often interact. Investigation of this problem is further complicated because strategies differ between spring and autumn migration (O'Reilly and Wingfield 1995, Yong et al. 1998).

Theoretical models of stopover duration provide quantitative and qualitative predictions that discriminate among species that attempt to maximize energy gain, minimize time enroute, or minimize energy expended during migration (Stephens and Krebs 1986, Alerstam and Lindström 1990). A review of field studies reveals that predictions of the time-minimization hypothesis accord with the stopover behavior of most small passerines and waders (Alerstam and Lindström 1990). Individuals in better condition (i.e., higher fat load) or that deposited fat quickly (i.e., higher consumption rate) had short stopovers.

Information regarding the stopover behavior of large-bodied migrants, species orders of magnitude larger than passerines and waders, is lacking. These data are potentially important because large birds have lower mass-specific metabolic rates than passerines and exhibit energy saving soaring flight (Kerlinger 1989, Hedenström 1993), two characteristics with direct relevance to models addressing migration behavior. Large birds should be less sensitive than small birds to the effects of body condition and consumption rates when deciding how long to remain at migratory stopovers.

I studied the stopover behavior of Bald Eagles (*Haliaeetus leucocephalus*), a large-bodied species (4–5.5 kg) that must stop to rest and feed during its 2000 km autumn migration across western North America (McClelland et al. 1994). First, I tested hypotheses that stopover duration of eagles is related to body condition and consumption rate. Second, I examined age-specific differences in stopover lengths. In previous studies, adult birds usually had shorter stopovers than juveniles, which tended to be in poor condition and needed additional time to replenish fat reserves before continuing migration (Serie and Sharp 1989; Ellegren 1991; Carpenter et al.

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1993a, b; Holmgren et al. 1993, Yong et al. 1998). Therefore, I predicted that if differences in stopover length existed between older and younger eagles, they would be due to differences in body condition or consumption rate. Age groups in better condition or which have higher consumption rates should have shorter stopovers.

METHODS

This study was conducted at Hauser Reservoir, a 23 km long impoundment of the upper Missouri River in west-central Montana (46° 41′ N, 111° 49′ W). Before 1989, Bald Eagles migrated quickly through the area during autumn, but after an introduced kokanee salmon (*Oncorhynchus nerka*) population proliferated. During the 1980s, hundreds of eagles began to congregate from October to December to feed on spawning and dead salmon. Over 7500 people visited the site annually to view eagles. The first 7 km of river below the dam and adjacent public shoreline was closed from mid-October to mid-December to protect eagles from human disturbance.

At least twice a week from mid-October to late November 1992–1994, several assistants and I captured eagles with padded, No. 3N double-spring leg-hold traps set around salmon carcass baits staked in shallow shoreline water (see Harmata 1985, McClelland et al. 1994 for detailed methodology). We watched trapping sites continuously from a distance of less than 1.6 km and removed eagles from traps within 5 min of capture.

Bald Eagles were banded, measured (Bortolotti 1984, Garcelon et al. 1985, McClelland et al. 1998), and aged (McCollough 1989). I did not rank body condition using the traditional index of mass/wing chord because wing chord differed among eagle age classes (Bortolotti 1984, McClelland et al. 1998), and most eagles captured during autumn at Hauser Reservoir had broken or heavily worn primary feathers. Instead, I ranked body condition using two other indices: (1) mass (g)/bill depth (mm) and (2) mass (g)/tarsal width (mm), measured anteriorly/posteriorly (AP; see Garcelon et al. 1985, McClelland et al. 1998). Because estimating body condition of migrants was species-specific (Spengler et al. 1995, Winker 1995), I used bill depth and tarsal width to correct for body mass because these two measurements best reflected size in Bald Eagles (see Bortolotti 1984, Garcelon et al. 1985). The relationship between bill measurements (culmen, bill depth) and body mass has also been used to rank body condition of soaring hawks (Gorney and Yom-Tov 1994). Bald Eagles of different ages that migrated through Montana had similar masses, bill depths, and tarsal widths (McClelland et al. 1998), so age-specific size did not confound interpretation of either condition index.

I used radio telemetry to estimate residence times because recapture and resighting data assume equal error among age or body condition groups. I fitted the first 20–25 eagles captured each season with radio transmitters (25 g; L. L. Electronics, Mahomet, Illinois) mounted ventrally to the two center retrices (Kenward 1978). It took 30–45 min to process each eagle and all were released within sight (< 1 km) of the trapping area. I used a hand-held, three-element yagi antenna to determine the presence or absence and location of radio-tagged eagles at least once a day during both daylight and evening hours (in roosts). Post capture residence time was calculated for each radio-tagged eagle by subtracting the date of capture from the date the eagle was last detected at Hauser Reservoir plus one day (Biebach et al. 1986).

Two observers recorded the foraging behavior of Bald Eagles from a vehicle parked 20–150 m from the primary salmon spawning and eagle foraging sites located along approximately 500 m of river. Observers used spotting scopes (20–60×) and binoculars (10×) to watch foraging eagles. Observations were made at least three times per week from late October to mid-December 1992–1994 in each of two time periods: 0.5 h before sunrise to noon and noon to 0.5 h after sunset. Foraging eagles were aged (juvenile; 1.5, 2.5, 3.5 year old; adult) using plumage, cere, and eye coloration (McCollough 1989). Observers attempted to record every foraging attempt, and recorded the time and estimated the fraction of salmon consumed (0, ⅓, ⅔, whole). Observations of individual foraging bouts began when eagles secured a salmon and ended when the salmon was consumed, dropped, or lost to a pirating conspecific.

In 1994 I collected 11 spawning salmon with a dip net and 11 salmon carcasses along the shoreline to determine caloric content. Each salmon was weighed in the field (wet, nearest 25 g) and frozen. In the laboratory, salmon were thawed, dried to constant weight (nearest g) in a convection oven (50–60° C), and ground into a homogenate using a Waring blender. Caloric content of duplicate samples from each salmon was determined using a semi-micro bomb calorimeter (Parr, model 1411). Forty salmon carcasses (20 of each sex) were also weighed (nearest 25 g) each autumn to obtain mean annual mass. Mean mass of live salmon (1992–1994) was obtained from state fisheries biologists.

Mass of salmon carcasses was similar among years (ANOVA: $F = 0.50$, df = 2, 117, $P > 0.05$). I used mean mass of live (1992: 1055 g, $n = 203$; 1993: 1101, $n = 63$; 1994: 1073 g, $n = 85$) or dead (1992: 831 g, $n = 40$; 1993: 883 g, $n = 40$; 1994: 860 g, $n = 40$) salmon multiplied by mean caloric content (live: 0.86 kcal/g, $n = 11$; carcass: 0.71 kcal/g, $n = 11$) and the fraction of salmon consumed to determine energy gain for each foraging attempt. I estimated consumption rates of Bald Eagles feeding at Hauser Reservoir on a sample of 3182 foraging attempts over 38 days of observation. Following the methods of Stalmaster and Gessaman (1984), I estimated mean daily energy intake for each eagle age class by dividing the total daily energy intake of each age class by the maximum daily count of similarly aged eagles recorded at one hour intervals during foraging observations.

Once a week from late September through December 1992–1994, a four person team conducted surveys by motorboat to estimate the number of eagles congregating at Hauser Reservoir. Surveys began between 09:00 and 10:00 MST. The boat travelled at 5–10 kph and at least three observers independently counted eagles. Counts were averaged to produce the survey total. I also determined relative prey abundance by counting the number of salmon carcasses on and within 2 m of two shoreline transects (1.6 km total) in the primary spawning reach. Using a headlamp, I counted carcasses 1.5 h before sunrise the day of eagle surveys.

When necessary, I transformed (log and square root) data (residence times, condition indices, consumption rates) prior to analyses (SPSS, Inc. 1998, version 8.0) to achieve normal distributions (Kolmogorov-Smirnov test) and homogeneity of variances (Levene's test). I have reported untransformed means (± 1 SE) in text, tables, and the figure to facilitate interpretation. I used ANOVA and *t*-tests to compare means (condition indices, consumption rates, capture dates) among or between age groups (all age classes or juveniles vs older eagles), respectively. Simple linear regression was used to detect relationships between post capture residence time and (1) body condition, (2) date of capture, and (3) time of capture. Simple linear regression was also used to examine the relationship between weekly counts of eagles and salmon. I used χ^2 tests to analyze two departure conditions: eagles leaving day of capture versus other eagles by age class and by crop condition.

RESULTS

Each year migrant Bald Eagles began to congregate at Hauser Reservoir in early October; weekly counts of both eagles and kokanee salmon peaked in mid-November. Each year the number of eagles and salmon were highly correlated (Fig. 1). Despite the ten-fold fluctuation in peak number of salmon carcasses among years, peak number of eagles was similar from 1992–1994.

We captured 99 eagles at Hauser Reservoir from 1992–1994. Not one eagle was recaptured within or across years. Most (86%) of the eagles we radio-tagged ($n = 68$) were captured before peak salmon counts, and overall residence time following capture averaged 10.4 (1.4) days. Radio-tagged eagles departed the stopover site continuously throughout each autumn. In 1992 marked eagles ($n = 23$) left on 17 different dates; in 1993 marked eagles ($n = 20$) left on 16 different dates; and in 1994 marked eagles ($n = 25$) left on 17 different dates. Few (9%) radio-tagged eagles, all of which were juveniles, remained at Hauser Reservoir into December. Latest departure dates of radio-tagged eagles were 14 December 1992, 25 November 1993, and 9 December 1994. Most (> 90%) of the reservoir had frozen by mid- to late December and fewer than 15 eagles remained in the area during winter.

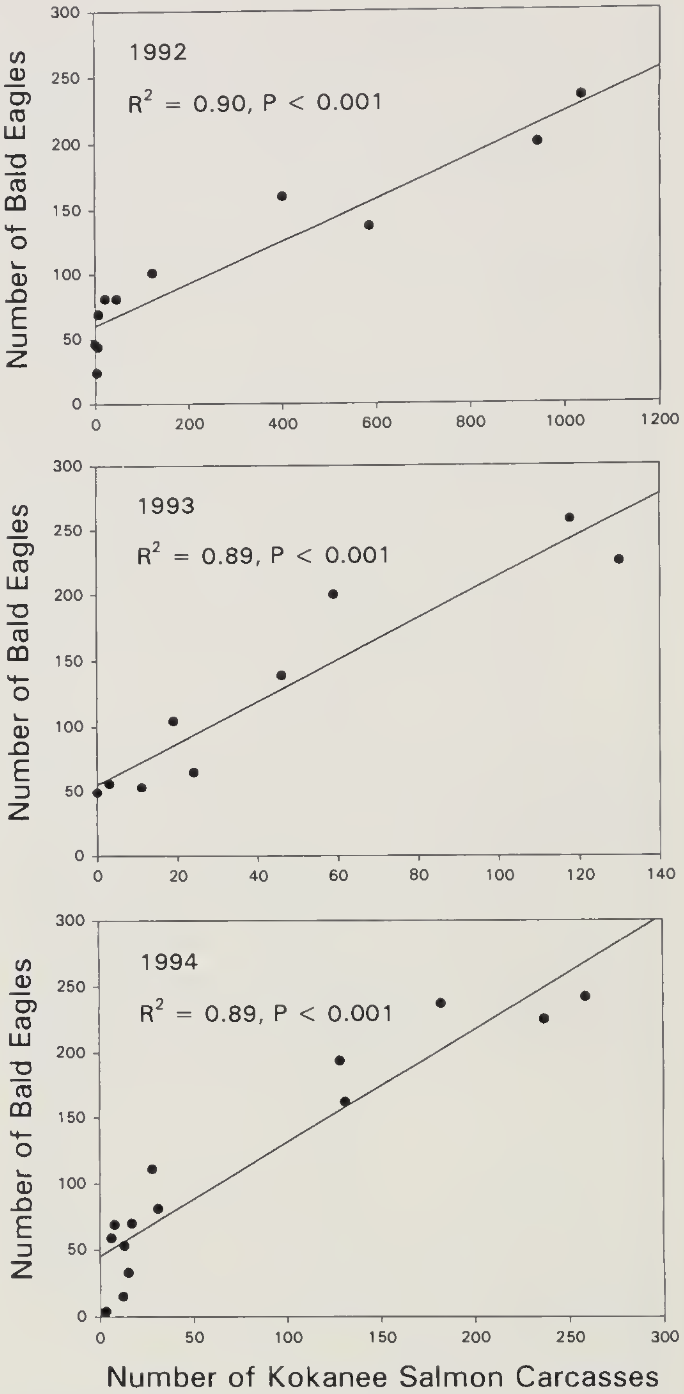

FIG. 1. Relationship between weekly number of Bald Eagles and kokanee salmon carcasses at Hauser Reservoir, Montana. Note that scales on x-axes differ.

Post capture residence times of radio-tagged eagles were similar among years (Table 1), so yearly data were combined for other analyses. After capture, juveniles remained at Hauser Reservoir significantly longer than

TABLE 1. Post capture residence times and consumption rates of Bald Eagles radio-tagged at Hauser Reservoir, Montana. Age classes: juvenile (JUV); 1.5, 2.5, 3.5 year old; adult (AD). Sample size for consumption rates is number of days foraging was observed.

	Residence time (days)		Daily consumption rate (kcal/eagle)	
	$\bar{x}$ (SE)	*n*	$\bar{x}$ (SE)	*n*
Year[a]				
1992	9.7 (2.4)	23	536 (33)	14
1993	13.9 (2.6)	20	540 (42)	13
1994	8.4 (2.3)	25	552 (24)	11
Age[b]				
JUV	14.5 (1.9)	41	457 (36)	38
1.5	4.7 (2.1)	14	453 (36)	37
2.5	4.2 (2.6)	6	576 (52)	37
3.5	4.0 (1.3)	5	452 (63)	31
AD	1.5 (0.5)	2	703 (42)	38
Sex[c]				
Male	10.0 (1.7)	45		
Female	11.3 (2.5)	23		

[a] Residence time: $F = 2.11$, df = 2, 65. $P > 0.05$; Consumption rates: $F = 0.04$, df = 2, 35, $P > 0.05$.

[b] Residence time: juveniles versus older eagles: $t = 4.58$, df = 66, $P < 0.001$; Consumption rates: $F = 6.02$, df = 4 and 176, $P < 0.001$ (AD > JUV, 1.5 and 3.5 year olds).

[c] $t = 0.44$, df = 66, $P > 0.05$.

TABLE 2. Body condition indices of Bald Eagles congregating at Hauser Reservoir, Montana. Age classes: juvenile (JUV); 1.5, 2.5, 3.5 year old; adult (AD).

	Mass (g)/Bill depth (mm)[a]		Mass (g)/Tarsus AP (mm)[b]	
	$\bar{x}$ (SE)	*n*	$\bar{x}$ (SE)	*n*
Juv	138.0 (3.5)	21	281.9 (6.0)	19
1.5	136.7 (3.4)	14	278.0 (6.2)	14
2.5	141.1 (4.4)	6	276.0 (10.4)	6
3.5	132.7 (6.9)	5	263.7 (9.7)	5
AD	120.3 (5.2)	2	243.5 (1.8)	2

[a] Juveniles versus older eagles: $t = 0.55$, df = 46, $P > 0.05$.

[b] Juveniles versus older eagles: $t = 1.22$, df = 44, $P > 0.05$.

older eagles (Table 1). The four older age classes had similar residence times following capture and were combined to increase statistical power. Older eagles left Hauser Reservoir the day of capture more often than juveniles ($\chi^2 = 7.41$, df = 1, $P = 0.007$), although no trend existed within the older age group: 1.5 year old (36% left day of capture), 2.5 year old (67%), 3.5 year old (0%), and adult (50%). I excluded eagles that left the day of capture to reduce the potential effect of age-specific handling stress and reanalyzed the comparison between age groups. Older eagles still had shorter residence times following capture than juveniles ($t = 3.07$, df = 52, $P = 0.003$). Residence times were similar for male and female eagles ($t = 0.44$, df = 66, $P > 0.05$; Table 1).

The body condition indices of radio-tagged juvenile eagles were similar to those of radio-tagged older eagles (Table 2). No relationship existed between post capture residence time and either condition index for the entire eagle sample (mass/bill depth: $R^2 = 0.01$, $P > 0.05$, $n = 48$; mass/tarsus AP: $R^2 = 0.06$, $P > 0.05$, $n = 46$) or for each age group (mass/bill depth: juveniles: $R^2 = 0.01$, $P > 0.05$, $n = 21$; older eagles: $R^2 = 0.10$, $P > 0.05$, $n = 27$; mass/tarsus AP: juveniles: $R^2 = 0.03$, $P > 0.05$, $n = 19$; older eagles: $R^2 = 0.09$, $P > 0.05$, $n = 27$). However, some eagles were captured with full crops (> 500 g), which may have added a large amount of variation to the condition estimates. To eliminate this potential bias, I repeated regressions using only eagles captured with empty crops. A significant relationship between post capture residence time and body condition (mass/tarsus AP) was evident, but the amount of variation explained was low (mass/bill depth: $R^2 = 0.01$, $P > 0.05$, $n = 32$; mass/tarsus AP: $R^2 = 0.14$, $P = 0.021$, $n = 31$). More importantly, the trend was opposite that expected: eagles in good condition stayed longer after capture than those in poor condition. Eagles captured with full, half full, or empty crops were equally likely to depart Hauser Reservoir the day of capture (juveniles: $\chi^2 = 4.53$, df = 2, $P > 0.05$; older eagles: $\chi^2 = 3.95$, df = 2, $P > 0.05$).

Although we captured juvenile eagles earlier during the season than older eagles ($t = 2.51$, df = 66, $P = 0.014$), date of capture explained little variation in post capture residence time for all eagles combined ($R^2 = 0.10$, $P = 0.005$, $n = 68$), or for each age group (juveniles: $R^2 = 0.01$, $P > 0.05$, $n = 41$; older eagles: $R^2 = 0.09$, $P > 0.05$, $n = 27$). The time of day of capture, a possible indicator of early morning foraging and recent mass gain that can affect estimates of condition (see Winker et al. 1992), was unrelated to post capture residence time for all eagles ($R^2 = 0.00$, $P > 0.05$, $n = 68$), or for each age group (juveniles: $R^2 = 0.00$, $P > 0.05$, n

TABLE 3. Mean (SE) consumption rates (kcal/eagle/day) of Bald Eagles feeding on kokanee salmon at Hauser Reservoir, Montana. Values were calculated for each week and dates shown correspond to mid-week. Sample size is number of days foraging was observed.

	Date[a]					
Year	11/1	11/8	11/15	11/22	11/29	n
1992	419 (16)	601 (71)	526 (74)	560 (69)	504 (128)	14
1993	483 (190)	573 (75)	609 (51)	427 (102)	617 (96)	13
1994	509 (12)	552 (64)	806 (190)	510 (121)	387 (113)	11

[a] $F = 186$, 4, 32 df, $P > 0.05$.

= 41; older eagles: $R^2 = 0.07$, $P > 0.05$, $n = 27$).

Mean daily consumption rates of eagles feeding on salmon did not differ among years (Table 1) or among days within years (Table 3). All yearly data were combined to estimate mean daily consumption rates for each eagle age class. High density and frequent movement of eagles at Hauser Reservoir made it difficult to locate and record foraging behavior of radio-tagged individuals. Therefore, I followed the methods of Loria and Moore (1990) and calculated consumption rates of similarly aged eagles and used those values as intake estimates for each age class of radio-tagged eagles. Adult eagles had higher mean daily consumption rates ($F = 6.02$, df = 4, 176, $P < 0.001$) than juveniles, 1.5 year old, and 3.5 year old eagles (Table 1).

DISCUSSION

Body condition of Bald Eagles at capture does not predict post capture residence time during autumn migration. In contrast, body condition of migrating ducks, shorebirds, and passerines correlates with duration of autumn stopovers (Cherry 1982, Biebach et al. 1986, Dunn et al. 1988, Serie and Sharp 1989, Ellegren 1991). These species usually gain a large percentage (40–60%) of normal body mass at stopovers to offset energetic costs associated with heavy wing-loading, migration using energetically expensive flapping flight, and long range movements. However, eagles have low mass-specific metabolic rates, minimize time spent foraging during the nonbreeding season (Stalmaster and Gessaman 1984), have low wing-loading, and migrate by energy efficient thermal soaring and gliding (Kerlinger 1989; Hedenström 1993, 1997). Eagles can also withstand days of fasting after gorging on salmon. This favorable combination of physiological and morphological attributes reduces the importance of gaining mass at stopovers, which may give eagles flexibility when deciding to resume migration.

Juvenile Bald Eagles stayed at Hauser Reservoir significantly longer following capture than older eagles. When similar age effects existed in other species, older birds were in better physiological condition (Serie and Sharp 1989, Ellegren 1991, Yong et al. 1998). However, eagles of different age classes were in similar condition, which further supported the pattern that body condition has little effect on stopover behavior. Hedenström (1997) reported that juvenile eagles migrated slower than older eagles from Europe to Africa, a pattern that might be caused by longer stopovers.

In contrast to other studies on fall migrants (e.g., Ellegren 1991, Yong et al. 1998), consumption rates, an indicator of mass gain, did not explain age-specific stopover behavior of Bald Eagles. Although juvenile and 1.5 year old eagles had similar daily consumption rates, these two age groups differed in post capture residence times. Interestingly, 1.5 year old eagles exhibited stopover behavior similar to older eagles. Several factors may have accounted for this pattern: experience gained during previous migrations (see Hedenström 1997), age-specific differences in muscle development, or age-specific expression of genetically-controlled impulses. However, annual mortality of juveniles and 1.5-year old eagles was similar (Harmata et al. 1999), and cannot account for such a striking age effect in stopover behavior.

Some species establish temporary feeding territories and/or exhibit interference competition at migratory stopovers (Rappole and Warner 1976; Lindström et al. 1990; Moore and Yong 1991; Carpenter et al. 1993a, b). Under these circumstances, poor competitors, usually juveniles, have low consumption rates, which causes them either to leave densely populated stopovers quickly in search of unoccupied areas or to have longer stopovers as they attempt to replace fat reserves. Dominance in Bald Eagles is based not on age but size (Garcelon 1990), and females are larger than males (Bortolotti 1984, Garcelon et al. 1985). The high incidence of food piracy [> 45% of foraging attempts (Restani 1997)] among foraging eagles at Hauser Reservoir suggests that stopover behavior should differ between subordinates (males) and dominants (females), yet residence time following capture was not sex-specific. The superabundant prey base may compensate for food lost to pirating conspecifics and thus support even poor competitors (see also Stalmaster and Gessaman 1984).

I found no correlation between date of capture and post capture residence time. This result was unexpected because post capture residence time of Bald Eagles at an autumn concentration in nearby (270 km) Glacier National Park, Montana was negatively correlated with capture date (McClelland et al. 1994). Two factors might have accounted for the difference between our studies. First, more eagles were radio-tagged at Hauser Reservoir before eagle numbers peaked compared to those tagged at Glacier National Park ($\chi^2 = 10.39$, df = 1, $P = 0.001$; McClelland et al. 1994: fig. 10). Whether eagles captured late in the season at Glacier had just arrived at the concentration or had been there for several days and were preparing to depart could not be determined. Second, 7 of 9 December departures from Glacier were of eagles captured in December, whereas I did not capture eagles past November. These differences in sampling may have created a false impression of seasonal effects.

Body condition of Bald Eagles did not correlate with post capture residence time, a result consistent with the hypothesis that ecophysiology of this large species (e.g., low mass-specific metabolic rate, migration using soaring flight) influences stopover behavior. Body condition and consumption rates did not explain the significant difference in stopover behavior between juveniles and older eagles. Resource depression was not a reason for eagles to leave Hauser Reservoir because consumption rates remained constant. Most eagles (94%) continued their migration in November, weeks before salmon abundance dropped in December. Eagles left the stopover continuously during autumn, rather than in large groups on certain days.

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GUTTURAL CALLS OF BLUE-FRONTED AMAZONS: STRUCTURE, CONTEXT, AND THEIR POSSIBLE ROLE IN SHORT RANGE COMMUNICATION

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ABSTRACT.—Structural variability of guttural calls of Blue-fronted Amazons (*Amazona aestiva*) was examined and the contexts in which they were given discussed relative to the role these vocalizations might play in short-range communication. Recordings were obtained at the Chancaní Reserve, Córdoba, Argentina, during breeding and non-breeding seasons. Guttural calls were given year round, but were more common during the non-breeding season when most of the individuals were interacting in flocks. Gutturals were detected when perched parrots contacted each other, during take-offs, landings, complex flock flying maneuvers, and feeding sessions. Guttural calls were subdivided into four types based on structure, but none of these types could be clearly assigned to a specific context. Structural variation in guttural calls was continuous rather than discrete, with the variability within and among individuals being similar. Many guttural notes graded into one another and were combined with other vocalizations. Gutturals were brief, had sudden onset, wide bandwidth, and low intensity. Gutturals could be regarded as short-range calls because of their large structural variability (fewer restrictions of sound attenuation and degradation) and low intensity (decreased attraction of predators). They were also produced by large flocks, probably as a means of maintaining contact, enhancing group spacing, and coordinating movements of individuals. *Received 11 Feb. 1999, accepted 19 Oct. 1999.*

Several parrot species have rather complex vocal repertoires (Farabaugh and Dooling 1996), with different vocalizations used in specific contexts (Saunders 1983, Martella and Bucher 1990, Fernández-Juricic et al. 1998a). They exhibit recognition of conspecifics (Rowley 1980, Saunders 1983, Wanker et al. 1998), vocal dialects (Wright 1996), and vocal mimicry (Cruickshank et al. 1993). Some call sequences structurally and functionally resemble passerine songs (Farabaugh et al. 1992, Fernández-Juricic et al. 1998c). Although previous studies have contributed to our understanding of parrot vocalizations, little is known about their structural variability or possible roles in social organization, particularly in wild populations.

The Blue-fronted Amazon (*Amazona aestiva*) is an interesting species because of its large structural and contextual vocal variability (Fernández-Juricic et al. 1998c) and its endangered status in many areas of its range (Bucher et al. 1992). Its vocal repertoire encompasses at least nine vocalizations, many of which are produced in different contexts (Fernández-Juricic et al. 1998c). The most commonly uttered call is the *wakwak,* which is associated with several situations (alarm, flight, contact) and is given along with other vocalizations, such as *wawawawa,* transitions, *gugugu,* and gutturals. Guttural calls are variable in frequency and time, especially when used in close proximity to other individuals (Fernández-Juricic et al. 1998c); however, structure, variability patterns, and contexts of these vocalizations remain poorly known.

This study has three main purposes: (1) to analyze the structural variability of guttural calls, (2) to determine the contexts of vocalization, and (3) to evaluate the hypothesis that guttural calls may be used as short-range signals in the forest habitats of this species. Depending upon habitat structure, animal vocalizations may withstand attenuation and degradation (Morton 1975, Wiley and Richards 1982, Forrest 1994). In closed habitats, the acoustic adaptation hypothesis (Rothstein and Fleischer 1987, Brown and Hanford 1996) predicts that for long distance signals animals should use long tonal or whistled sounds and avoid repeated elements. Short-range communication signals are expected to show higher structural variability because of the fewer restrictions in environmental sound propagation channels (Marler 1967, Morton 1982).

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Other differences might include shorter duration, sudden onset, broader frequency range (Clemmons 1997), and low intensity to reduce auditory detection by predators (Wiley 1976, Wiley and Richards 1982). Short-range signals are predicted to function as contact calls because they are vocalized more frequently by interacting social units than by solitary individuals (Smith 1986, Mathevon 1997).

METHODS

Study area.—Samples of Blue-fronted Amazon guttural calls were recorded in the Chancaní Reserve, Córdoba, Argentina (65° 26′ W; 30° 22′ S), a 4920 ha area of Chaco habitat where the dominant plant community comprises the quebracho-blanco forest (*Aspidosperma quebracho-blanco*; Carranza et al. 1992). Annual precipitation ranges from 300–550 mm (Capitanelli 1979).

Approximately 50 individuals inhabit the reserve, which appears to be isolated from other suitable forest patches and are at the southern limit of the species' range (Fernández-Juricic et al. 1998b).

The reserve was visited five times during 1993 and 1994. Sampling was concentrated in the morning (from 30 min before sunrise to mid-morning) and afternoon (in the 3 h before sunset), resulting in 100 hours of observation (10 recording h), using the techniques of Altmann (1974).

Vocalizations and sonograms.—Vocalizations were recorded with an Uher 4000IC tape recorder at a speed of 19.05 cm/s and a directional microphone (Electro-Voice Model 644). A 16-bit stereo Sound Blaster card was used to digitize sounds up to 22.05 kHz. Sonograms were made with Spectrogram 2.3 software, with broadband analyses [FFT window width: 12 milliseconds (ms)]. The following structural variables were measured (Fig. 1): low frequency [the lowest frequency record in the sonogram, in Hertz (Hz)], high frequency (the highest frequency record in the sonogram, in Hz), frequency range (bandwidth, the difference between the highest and lowest frequencies, in Hz), energy concentration (the frequency at which the acoustic energy is strongest, in Hz), number of harmonics (number of frequency band multiples of the fundamental), number of frequency modulations, and duration (in ms).

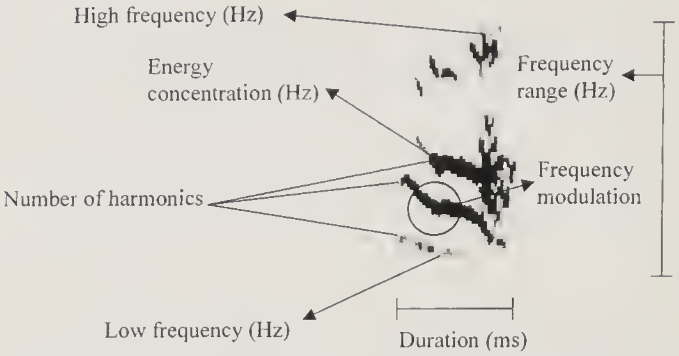

FIG. 1. Structural traits measured on Blue-fronted Amazons (*Amazona aestiva*) guttural calls: low frequency [the lowest frequency record in the sonogram, in Hertz (Hz)], high frequency (the highest frequency record in the sonogram, in Hz), frequency range (bandwidth, the difference between the previous variables, in Hz), energy concentration (indicates the frequency where most of the acoustic energy is concentrated, in Hz), number of harmonics, number of frequency modulations, and duration (in ms).

Because Blue-fronted Amazons were sexually indistinguishable and the threatened status of the Chancaní population did not allow tagging individuals, we could not reliably distinguish between individuals. To estimate inter-individual acoustic variability and to reduce the effects of pseudoreplication (Hurlbert 1984), we proceeded as follows: recordings were primarily made when birds were flying to feeding grounds and roosting areas; when feeding; when arranging cavities to be used as nests; when perching before, during, and after social interactions; and when fleeing from intruders (such as the observer). Flocks were identified, mapped, and acoustically sampled in distinct recording bouts. Each bout was assigned to a specific flock so that we could identify bouts from different groups that were not overlapping. From each of these different flock bouts, we collected only one guttural call belonging to one individual from each group for statistical analysis. This procedure was repeated throughout the study period so as to get a similar number of guttural calls for each sampling period and day, and as many different guttural calls as possible (total sample size = 80 calls). Hence, the sampling unit was a single individual within a flock, regardless of the number of individuals within the flock. This method reduced the probability of taking multiple samples from the same individual and biasing the results. A similar selection procedure was used to analyze the other vocalizations used for comparison.

Although intra-individual variability could not be estimated because of the restriction against tagging individuals, we made a rough estimate. On two consecutive days in four different zones of the reserve, we were able to record several guttural calls belonging to four different parrots (19, 15, 11, and 14 calls, respectively). All four parrots were recorded within flocks of at least four individuals. The variability within the calls of these four parrots was then compared to that among individuals (35 notes randomly selected from the pool of 80 calls) by a test for differences between variances (Sokal and Rohlf 1981), by which $F = S^2_1/S^2_2$, with $(n_1 - 1)$ and $(n_2 - 1)$ degrees of freedom, and S^2_1 and S^2_2 were the larger and the smaller variances, respectively. Although the estimate of intra- vs inter-individual variability could have been biased because of a small sample size, our intention was to assess whether the variability in guttural calls stemmed from intra-individual variability (individuals using different vocalizations) or inter-individual variability (each individual using a single vocalization).

TABLE 1. Structural features of 80 Blue-fronted Amazons' guttural calls recorded in the Chancaní reserve, Córdoba, Argentina. Frequency variables are expressed in Hz, and duration in ms.

	Low frequency	High frequency	Bandwidth	Duration	Concentration of acoustic energy	Number of harmonics	Number of frequency modulations
Mean	634.46	3447.35	2813.51	126.50	1771.61	4.56	4.31
SD	238.37	973.83	1077.84	33.73	263.91	1.72	2.44

Structural and contextual analysis.—Guttural calls were first characterized by mean and standard deviation (SD) of the acoustic traits (Fig. 1). A Principal Components Analysis (PCA) was performed to generate a reduced set of variables that account for most of the variability in the original data set. Low and high frequency were excluded from the analysis because they were highly correlated with bandwidth. We employed a correlation matrix because variables were on different measurement scales. Only those PCA factors with eigenvalues greater than 1 were selected (Kaiser criteria; StatSoft, Inc. 1996). The factors identified by the PCA were then used to assign guttural calls to one of four arbitrary types (corresponding to the four quadrants determined by the arrangement of the two first classification factors). We also examined the other PCA factors for grouping of gutturals. Each guttural call type identified was then related to the contexts of vocalization.

The following terms were adopted to describe the calls (Fernández-Juricic et al. 1998c): note, a short sound not interrupted by a silence; complex syllable, a group of different notes encompassing coherent units in the sonogram; bands, frequency sectors in which acoustic energy is concentrated; and transitions, a note with less intensity in relation to other guttural calls given at the same distance as indicated by a fainter trace in the sonogram.

Guttural calls were compared with six other types of calls (*wakwak, wawawawa*, transition to wakwak, *gugugu, grruíp*, and songs; described in Fernández-Juricic et al. 1998c) with corrected coefficients of variation because of low sample sizes ($CV' = (1 + 1/4n) \times CV$) and a test for differences between variances (Sokal and Rohlf 1981). The following traits were considered in the comparisons: energy concentration, high frequency, and low frequency.

An ANOVA was employed to analyze mean duration and bandwidth of guttural calls with regard to four calls: *wakwak, wawawawa* (structurally different and frequently used in alarm situation), *gugugu*, and songs (structurally similar to gutturals, but employed over long distances). Residuals of the analysis were normally distributed and had equal variance.

Guttural call amplitudes were compared by *t*-test with the most common Blue-fronted Amazon vocalization: *wakwak*. Call intensity [decibels (dB)] was measured with the software Wave Editor 1.03. Because intensity can be highly biased by attenuation/reverberation effects produced by slight differences in recording distances (Wiley and Richards 1982), we included in the analysis recordings taken at 100 ± 5 m from the source (usually flying parrots).

To analyze whether gutturals would be playing a more relevant role in the transmission of information at short distances as the number of interacting individuals increased, we assessed the variability in five structural properties of guttural calls (low frequency, high frequency, bandwidth, energy concentration, and duration) in flocks of 1, 2–3, and more than 4 individuals by means of the same test for differences between variances discussed before (Sokal and Rohlf 1981). All statistical analyses were conducted with STATISTICA 4.5 software.

RESULTS

Structural characteristics.—Guttural calls consistently share five characteristics: short duration, high structural diversity (several structurally different notes), frequency modulation (most analyzed frequency bands showed upward and downward shifts), broad bandwidth, and sudden onset (Table 1, Fig. 2). Structurally, gutturals were highly variable and included notes that were modulated over a wide frequency range either upwards or downwards (Fig. 2A–C), notes slightly modulated (Fig. 2D–F), complex and long-duration notes (Fig. 2G), buzz sounds (Fig. 2H), barely audible sounds (Fig. 2I), short notes with blurred or noisy frequency structure (Fig. 2J), and complex syllables composed of two distinct units (Fig. 2K).

The Principal Component Analysis generated two components that accounted for nearly 76% of the observed variance (Table 2). The first factor was composed of bandwidth, number of harmonics, and number of modulations; the second factor included the concentration of acoustic energy (Table 2). Guttural calls were assigned to one of four types according to their positions in the four quadrants produced by the PCA axes (Fig. 3; Q1, Q2, Q3, and Q4). Axes beyond PC1 and PC2 were not important for grouping guttural calls. Most guttural notes (Q1 and Q3) seem to have narrow bandwidths with little modulation

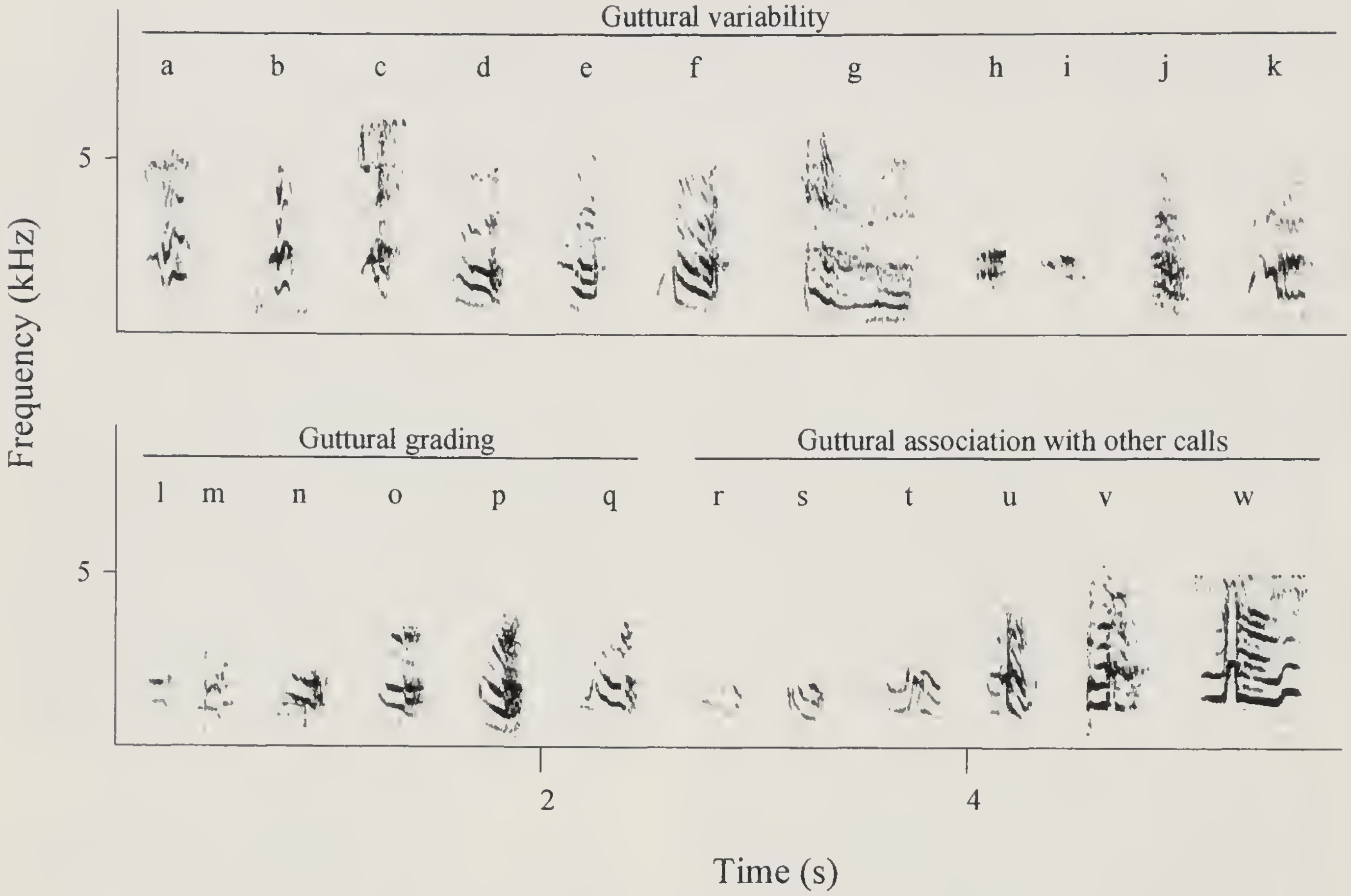

FIG. 2. Guttural calls of Blue-fronted Amazons (*Amazona aestiva*) recorded in the Chancaní Reserve, Córdoba, Argentina. Calls given when perching or taking off but not during flights (A–C), calls produced by flying or perching parrots (D–F), calls given by isolated individuals contacting a large flock, during coordinated take-offs, and while perching (G–K), a sequence depicting a simple graded bout of gutturals given by a single individual (L–Q), sequence (R–W) showing the association between gutturals (R–S) and other Blue-fronted Amazon calls: transitions to *wakwak* (T–U), and *wakwaks* (V–W).

(Fig. 2D–F). Much of the overall structural variation appears to be continuous rather than discrete (Fig. 2), resulting in no clustering of notes (Fig. 3).

Intra- vs inter-individual variation.—The structural variability of guttural calls within and among individuals was similar (Fig. 4). Eighty percent of the multiple variance comparisons were not significant ($F_{10,34}$ = 1.048–2.083, $P > 0.05$); only four contrasts showed that the variability among individuals (G) was

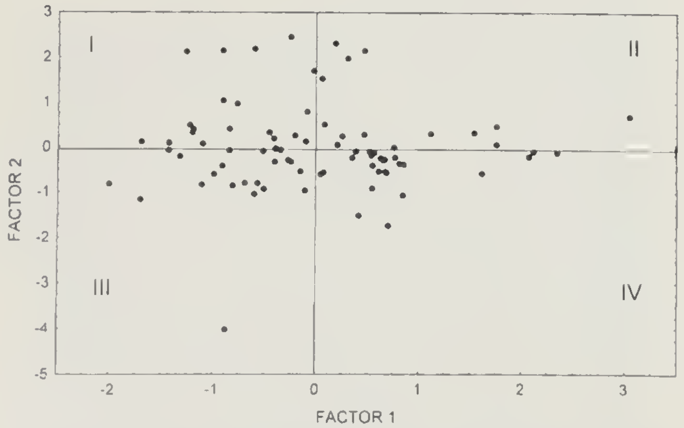

FIG. 3. Individual guttural calls of Blue-fronted Amazons (*Amazona aestiva*) and their positions along the first two Principal Component axes.

TABLE 2. Correlations between the first two Principal Components and the original variables of 80 guttural calls of Blue-fronted Amazons *Amazona aestiva*. Significant correlations ($P < 0.05$) among variables and factors are marked with *.

	Factor 1	Factor 2
Bandwidth	0.873*	0.003
Duration	0.654	−0.224
Energy concentration	−0.025	−0.980*
Number of harmonics	0.905*	0.098
Number of modulations	0.863*	0.036
Eigenvalue	2.75	1.02
Variance (% total explained)	55.09	20.47
Cumulative Variance (%)	55.09	75.56

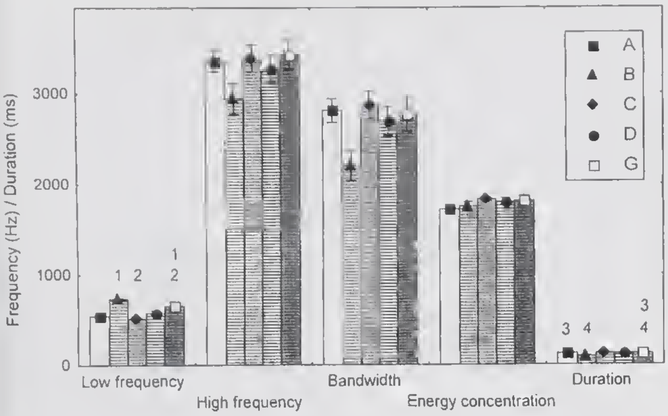

FIG. 4. Intra- and inter-individual acoustic variability in guttural calls of Blue-fronted Amazons (*Amazona aestiva*). The variability of guttural calls belonging to four parrots (sample sizes: A = 15, B = 11, C = 14, D = 19) are compared to that of 35 randomly selected guttural notes (G) with a test of differences between variances. Columns with the same number indicate pairs of significantly different contrasts: B vs G, low frequency, $F_{10,34} = 4.78$, $P < 0.01$; C vs G, low frequency, $F_{10,34} = 4.14$, $P < 0.01$; A vs G, duration, $F_{10,34} = 2.7$, $P < 0.05$; B vs G, duration, $F_{10,34} = 3.2$, $P < 0.05$.

higher than that within individuals (individuals A–D; Fig. 4).

Contexts of vocalization.—Guttural calls were given year round, particularly in contexts related to contact among individuals. Guttural calls were most common in March (post-breeding) and May (non-breeding) when parrots spent much time together. In the breeding season, guttural calls were primarily restricted to communication within the pair.

Gutturals generally elicited a vocal response or aggregation from other parrots, as if they were affiliative sounds (Miller and Job 1992). They were heard in the following contexts: when perching and flying parrots were contacting and aggregating, during take-offs, during landings, during complex flocking maneuvers, and while feeding. Analyzing these contexts relative to the four classes of notes (Q1–4), we found that no structural note was exclusively recorded in a specific context; instead, they were given in all contexts (Table 3).

During the non-breeding period, individuals within flocks engaged in continuous and coordinated vocal contacts. Generally, flocks entered and left feeding areas gradually. Typically, two individuals arrived first, perched conspicuously, and stared at their conspecifics. As the rest of the flock flew toward the core sector vocalizing, these scouts (sensu Yamashita 1987) responded with several guttural notes. Unless flying parrots called, the two perching individuals remained silent, watching both the flock and their surroundings. After the arrival of all parrots, a chorus of gutturals began and increased in intensity until the groups departed.

Syntax.—During the vocalization of long guttural bouts, Blue-fronted Amazons usually started with a couple of soft notes or transitions that graded into clear guttural notes (Fig. 2L–Q). Such an assortment was produced primarily by isolated individuals. Gutturals were also given in a sequence with *wakwak* and *wawawawa* vocalizations (described in Fernández-Juricic et al. 1998c). A typical sequence, usually given by flying parrots, was guttural → transition to *wakwak* → *wakwak* → *wawawawa* and/or → *wakwak* modification (Fig. 2R–W).

Short-range signals.—We found that the structural variation of guttural calls (CVs) was greater than that of the other vocalizations (Table 4). In addition, when statistically com-

TABLE 3. Percentage of four Blue-fronted Amazons' (*Amazona aestiva*) guttural call morphs (Q1–4) given in different contexts during breeding and non-breeding seasons (both seasons pooled) at the Chancaní reserve, Córdoba, Argentina.

Context	Q1	Q2	Q3	Q4
solo-flying	10.53	7.69	18.18	11.54
flying-flock	5.26	7.69	9.09	19.23
solo-perching	5.26	15.38	13.64	3.85
perching-flock	21.05	23.08	18.18	26.92
takeoff-air aggregation	5.26	7.69	4.55	7.69
feeding	15.79	7.69	9.09	11.54
pre-flight	31.58	23.08	22.73	15.38
landing	5.26	7.69	4.55	3.85

TABLE 4. Coefficients of variations of seven Blue-fronted Amazons' vocalizations considering four structural traits: energy concentration, high frequency, bandwidth, and duration.

Vocalization	High frequency	Bandwidth	Energy concentration	Duration
wakwak	76.2	100.1	29.8	177.4
wawawa	78.9	90.5	74.2	134
transitions	52.9	81.5	17.3	108.1
gugugu	37.6	59.8	24.6	132.9
kakaka	236.3	276.4	101.6	306.4
grruip	28.7	35.9	12.8	42.2
Guttural calls	671.5	1021.1	439.7	747.1

paring the variances of the three frequency features (low frequency, high frequency, and bandwidth), guttural variability was greater (Table 5).

Guttural calls were briefer than *wawawawa, wakwak, gugugu,* and songs (ANOVA: $F_{4,126} = 39.15$, $P < 0.001$; guttural calls, 135.4 ± 40.5 ms; *wawawawa,* 353.9 ± 79 ms; *wakwak,* 243.2 ± 50.8 ms; *gugugu,* 253.2 ± 84.1 ms; songs 153.8 ± 100.8 ms); the latter four were frequently used for contact over long distances (Fernández-Juricic 1994). The bandwidth of gutturals was intermediate, larger than *gugugu* and songs (ANOVA, $F_{4,126} = 166.4$, $P < 0.001$; guttural calls, 3687.8 ± 603 Hz; *wawawawa,* 4805.3 ± 725.3 Hz; *wakwak,* 4802.5 ± 565.9 Hz; *gugugu,* 1405 ± 210 Hz; songs 1828.3 ± 542 Hz). Gutturals were also softer than the commonly uttered *wakwak* calls ($t = 13.143$, 42 df, $P < 0.001$; gutturals, 0.36 ± 0.03 dB; *wakwak,* 0.91 ± 0.02 dB).

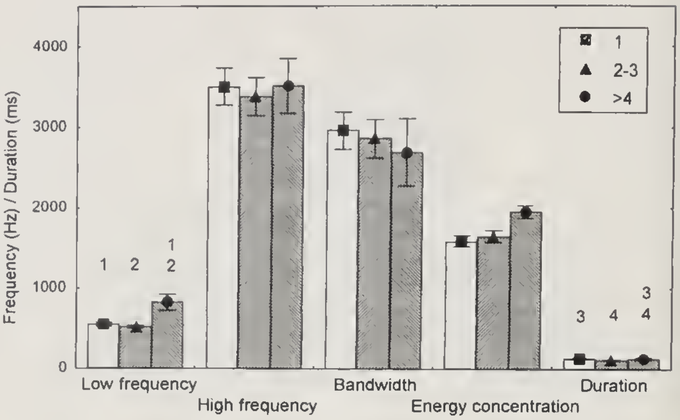

FIG. 5. Acoustic variability in guttural calls of Blue-fronted Amazons (*Amazona aestiva*) in relation to flock size categories (1, 2–3, more than 4 individuals, 15 randomly selected notes per category). Columns with the same number indicate pairs of significantly different contrasts: more than 4 vs 1, low frequency, $F_{14,14} = 4.02$, $P < 0.01$; more than 4 vs 2–3, low frequency, $F_{14,14} = 5.93$, $P < 0.01$; more than 4 vs 1, duration, $F_{14,14} = 2.7$, $P < 0.05$; more than 4 vs 2–3, duration, $F_{14,14} = 2.57$, $P < 0.05$.

The variability in guttural call duration and lowest frequency was greater for flocks larger than four individuals than for single individuals (Fig. 5). Low frequency and duration were the structural variables included in the significant contrasts (Fig. 5). The other traits (high frequency, bandwidth, and energy concentration) did not showed any significant difference among different sized social groups ($F_{14,14} = 0.678$–1.792, $P > 0.05$; Fig. 5).

DISCUSSION

Guttural calls can be regarded as highly variable. This variability apparently increases with flock size, with single individuals producing notes as different as those given by all the other flock members. Variability in parrot contact calls has also been described for *Amazona auropalliata,* in which geographic dif-

TABLE 5. Comparison of the variation in guttural calls and other Blue-fronted Amazon vocalizations. Sample sizes: guttural = 80, *wawawawa* = 20, *gugugu* = 12, *kakakaka* = 62, transition = 9, *wakwak* = 30, *grruíp* = 8. Shown are *F* values and significance levels of tests for differences between variances (Sokal and Rohlf 1981).

Comparison	Energy concentration	High frequency	Low frequency
Guttural–*wawawawa*	2.491 (*)[a]	3.387 (**)	3.937 (***)
Guttural–*gugugu*	11.479 (***)	36.391 (***)	9.226 (***)
Guttural–*kakakaka*	18.272 (***)	3.108 (***)	2.090 (**)
Guttural–transition	11.601 (***)	3.140 (*)	14.251 (***)
Guttural–*wakwak*	25.995 (***)	7.524 (***)	3.391 (*)
Guttural–*grruíp*	39.015 (***)	4.672 (*)	4.049 (*)

[a] * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

ferences are reflected in the acoustic properties of these calls (Wright 1996).

The results of this study further characterize guttural calls in structural terms: within and among individual variations are similar, some notes appear to grade into each other, gutturals are combined with other vocalizations in a specific order, and structural categories cannot be exclusively ascribed to specific contexts. No definite conclusion could be made to account for such structural variability, and further analyses are needed (particularly by means of playback tests). However, some preliminary conclusions (not mutually exclusive) can be drawn.

First, the structural variation in guttural calls might be associated with the transmission of different messages. In this case, specific structural variations would be associated with particular messages (Hailman et al. 1987, Smith 1997). Although some guttural types were more frequently recorded in specific circumstances, most types were given in all contexts. Second, different guttural calls might represent different functional categories. If so, each guttural type would have structural variation similar to other vocalizations of the Blue-fronted Amazon's repertoire (*wakwak, wawawawa,* etc.). However, the continuous variation in gutturals, along with the lack of complete specificity, indicates that these two hypothesis are not supported with the information available. Third, the degree of variation in guttural calls might result from the acoustic restrictions of short range communication (discussed below).

Variability in guttural vocalizations seems to be continuous rather than discrete. A continuous variability might allow individuals to take advantage of the situational context to support the behavioral message of the call (Morton 1982, Smith 1986). Such contextual variation could support different amounts of information within single or multiple calls (Marler et al. 1992, Armstrong 1995, Smith 1997). Thus, Blue-fronted Amazons might rely on contextual information because the guttural call types lack specificity.

Guttural types do not appear to be functionally distinct. The continuous variability of gutturals coupled with the variety of contexts in which they were given suggest that these vocalizations are a single acoustic and functional category that may serve to maintain vocal contacts among Blue-fronted Amazons. Guttural calls were more frequent during the non-breeding season, presumably as a result of larger and more dynamic flocks which, consequently, produced more interactions among individuals (Fernández-Juricic et al. 1998b). Thus, parrots might rely upon gutturals to inform other flock members of conditions when moving and foraging as a cohesive group (Smith 1986, 1997; Boughman 1997). Moreover, the continuous production of gutturals might enhance the coordination of flocks and spacing between individuals.

Guttural calls could be regarded as complex vocalizations. Complexity comes not only from structural diversity but also from the way in which vocal elements are combined (Smith 1997). Blue-fronted Amazons might use a combination of gutturals and other calls (*wakwak* and *wawawawa*) as a means of increasing the information contained in single guttural notes. Similarly, songs of Blue-fronted Amazons are formed by combinations of different calls with specific syntax rules (Fernández-Juricic et al. 1998c). Similar composite vocalizations with the arrangement of notes varying according to the context of vocalization have been found in other species (Hailman et al. 1987, Armstrong 1992), and could be important for aggregation during the non-breeding season.

The complexity of auditory signals may be greatly influenced by acoustic characteristics of the habitat and ultimately may affect social relationships. Close range signals are not influenced by as many acoustic restrictions as long range sounds (Marler 1967, Wiley and Richards 1982, Forrest 1994). Blue-fronted Amazons' guttural calls appear to serve as close range signals because of their large variability, broad bandwidth, short duration, rapid repetition, abrupt onsets, low intensity, and frequency modulation patterns. These characteristics would greatly limit the distance at which guttural calls could be detected. Because they are low intensity, they probably evolved to transmit messages across relatively short distances, such as contact situations (Wiley 1976). This sort of vocalization usually takes place in large social groups (Marler 1965), such as in this species' large flocks. Similar close range vocalizations have been encountered and simulated in Black-capped Chickadees (Clemmons 1997).

Given the high degree of acoustic variation coupled with the isolation of the population we studied, it could be predicted that Blue-fronted Amazons' guttural calls would vary between distinct populations, producing local variations or dialects (Krebs and Kroodsma 1980). Such local variability has been found in other *Amazona* parrots, such as *A. auropalliata* (Wright 1996). Future research should be oriented towards studying the guttural calls of other Blue-fronted Amazon populations to identify possible dialects.

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RED-NAPED SAPSUCKER NEST TREES IN NORTHERN ROCKY MOUNTAIN OLD-GROWTH FOREST

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ABSTRACT.—Throughout western North America, Red-naped Sapsucker (*Sphyrapicus nuchalis*) nests have been previously described primarily in trembling aspen (*Populus tremuloides*) with decay-softened wood. During 1974–1992, we located Red-naped Sapsucker nest trees (n = 125) in northwestern Montana old-growth coniferous forest that included widely scattered paper birch (*Betula papyrifera*). Sapsucker nests were in nine tree species (seven conifers). Most (68%) nest trees were live and 75% had broken tops. Western larch (*Larix occidentalis*) and birch were greatly over utilized compared to their availability. Larch nest trees (n = 84) were large [mean DBH = 69 ± 20.95 (SD) cm]. Mean DBH of birch nest trees (n = 30) was 37 ± 8.42 cm. All Mountain Chickadee (*Poecile gambeli*) nests (n = 36) and 12 of 23 Red-breasted Nuthatch (*Sitta canadensis*) nests were in old sapsucker excavated nest holes. Wood of larch and birch is inherently harder than that of aspen (specific gravity = 0.48, 0.48, and 0.35 respectively), posing a potential obstacle for relatively weak excavators such as sapsuckers. However, the entire inner wood column of birch is susceptible to decay fungi and the durable bark is thin. In larch sapsuckers mitigated the difficulty by selecting trees with extensive heartwood decay (old larch) and by excavating in the upper bole (mean cavity height = 21.5 m), where the bark is thinner. External evidence of heartwood decay was present in 87% of larch and 86% of birch. Decay incidence increases with age in western larch forests, amplifying their value as habitat for sapsuckers and many other species. Perpetuation of old-growth western larch is an important component in the conservation of biological diversity. *Received 8 March 1999, accepted 24 August 1999.*

General ornithological references for the northern Rocky Mountains allude to the Red-naped Sapsucker's (*Sphyrapicus nuchalis*) nesting dependance on trembling aspen (*Populus tremuloides*), riparian woods, and orchards (Johnsgard 1986, Ehrlich et al. 1988), or on deciduous and mixed woodlands where poplar (*Populus* spp.) and birch (*Betula* spp.) are common (McGillivray and Semenchuck 1998). Sapsucker selection of trembling aspen (hereafter, aspen) nest trees in western North America has been well documented (Erskine and McLaren 1972, British Columbia; Crockett and Hadow 1975, Colorado; and Li and Martin 1991, central Arizona). In western Montana, Weydemeyer and Weydemeyer (1928) described the Red-naped Sapsucker as nesting most commonly in live aspen. Before our study, old-growth conifer stands in the western United States had not been included in the description of quality habitat for sapsuckers. Following our study, Tobalske (1992) studied habitat suitability related to Red-naped Sapsucker fledging success in part of our old-growth study area.

Our objectives were to (1) locate and describe active sapsucker nest trees in old-growth coniferous forest, (2) compare sapsucker nest trees to those of other woodpecker species, and (3) identify secondary cavity nesters that used old sapsucker holes. Preliminary results of our study were reported in McClelland and Frissell (1975) and McClelland and coworkers (1979).

STUDY AREA AND METHODS

Our study, 1974–1992, began at a time when the U.S. Forest Service had insufficient data for evaluating impacts of forest harvesting on cavity nesters in old-growth forests of the northern Rocky Mountains. We focused on the Coram Experimental Forest (approximately 48° 21′ N, 114° 00′ W), an International Biosphere Reserve encompassing 3019 ha (including a 324 ha natural area) in the Flathead National Forest, northwestern Montana (U.S. Forest Service 1979). Elevations range 1188–1615 m. Coram forest's climate is typical of similar terrain in the northern Rocky Mountain region (Hungerford and Schlicter 1984). About 70% of the Coram forest had not been cut and was classified as mature or old (H. Trechsel, pers. comm.). The old-growth component of the uncut forest was dominated by Douglas-fir (*Pseudotsuga menziesii*) and western larch (*Larix occidentalis*; hereafter, larch; U.S. Forest Service 1979). Some easily accessible large trees were selectively cut as early as 1916 and research oriented harvesting (clearcuts and selection cutting) began in the 1940s. During our study, previous clearcuts (16% of the CEF) supported young stands of

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conifers dominated by larch (too small for cavity nests), with isolated stems or small groves of paper birch (*Betula papyrifera*; hereafter, birch), and an occasional remnant conifer snag. Although mature groves of aspen were not present immediately within the old growth we examined, some were nearby in localized areas of the Flathead National Forest and Glacier National Park.

During May through August, 1974–1992, we searched old-growth forest at Coram for active cavity nests of all species, but here we focus on the Red-naped Sapsucker. We walked roads and trails, and randomly selected cross-country routes. By the end of 1992, all major old growth on the Coram forest had been searched. Within logged old-growth sites abutting existing old growth, cavity nests in remnant trees were recorded if they were discovered from the uncut stands we were searching. In nearby Glacier National Park and the Flathead National Forest, we hiked trails and cross-country routes selected to maximize observation of old-growth Douglas-fir/larch stands.

To find active woodpecker nests, we let the birds lead us to the active nest trees; we did not focus on any tree species or forest stand within the surveyed areas. We used visual cues (observation of an incubation exchange by adults, or a food carrying adult flying to and entering a hole), and auditory cues (vocalizations of young in the nest). During the two weeks before fledging, vocalizations of woodpecker nestlings, especially sapsuckers, sometimes carry 100 m or more (Kilham 1977). To find active nests of secondary cavity nesters [e.g., chickadees (*Poecile* spp.) and nuthatches (*Sitta* spp.)] we used similar visual cues, but without the advantage of auditory clues from the young. For all cavity nests, we recorded the nest as active only if incubation or the presence of young was confirmed. Nest status was observed from the ground. Near low nests, vegetative concealment was used to prevent disturbance. Easily accessible sapsucker nest trees were revisited the year following their first documented use. Time limitations required a choice between revisiting all previously located nest trees or searching for nest trees in previously unsurveyed portions of the study area. We chose to emphasize the latter.

At nest trees, tree condition was characterized by presence of dead wood and tree structure: intact top snag, broken top snag, broken top live, dead top live, or live top live. We also recorded tree species, diameter at breast height (DBH), tree height, percent canopy cover (ocular estimate), basal area of the surrounding forest (measured with a Spiegel Relaskop), nest height, azimuth of the nest opening, and number of prior nest holes. Presence of heartwood decay was confirmed by: (1) a conk (external fruiting body of heartwood-decay fungus; Parks et al. 1997); (2) swollen punk knots and resinosis (Boyce 1948, Partridge and Miller 1974, Manion 1981); (3) decayed heartwood visibly exposed in the nest opening, woodpecker feeding excavations, cracks, or wounds; (4) evidence of carpenter ant (*Camponotus* spp.) galleries within the tree (Sanders 1964); and (5) an old broken top or fire scar (Bull et al. 1997, Parks et al. 1997). We searched for cavity excavation chips on the ground at the base of each nest tree. Chips were examined for visible evidence of decay as described by Partridge and Miller (1974) and Parks and coworkers (1997; e.g., typical white "pockets" or bleached areas). The woodpecker species responsible for prior holes was identified using Headstrom's (1970) key and reliance on our 40 years experience observing woodpecker nest construction.

We did not sample the surrounding forest at each nest tree. However, the U.S. Forest Service concurrently sampled plots (32 ha, pooled) characterized as representative of Coram Experimental Forest's uncut forest. They recorded total tree counts by species and size. To enable a comparison of availability and nest-tree selection, we used their sample of trees at least 23 cm DBH (coincidentally, the smallest sapsucker nest tree DBH we found) to provide a crude indicator of potential nest-tree availability. Composition of the sample sites was: Douglas-fir (52% of all tree species present, mean DBH = 38 cm), subalpine fir (*Abies lasiocarpa*; 22%, 28 cm), Engelmann spruce (*Picea engelmannii*; 12%, 33 cm), larch (11%, 49 cm), western hemlock (*Tsuga heterophylla*; 1%, 32 cm), lodgepole pine (*Pinus contorta*; 1%, 30 cm), western white pine (*Pinus monticola*; 1%, 33 cm), western red cedar (*Thuja plicata*; <1%, 37 cm), and birch (<1%, 33 cm; R. Benson, pers. comm.). Birch were isolated within the old growth, primarily in riparian zones. We recognized that old-growth forest composition outside the Coram forest might differ from the U.S. Forest Service Coram study plots. Therefore, we used only those sapsucker nest trees found on the Coram forest to compare with the expected values derived from the Coram forest sample sites. χ^2 goodness of fit analyses were used to compare sapsucker nest trees with available trees. Resulting standardized residuals (Everitt 1992) were used to further illustrate differences.

In comparisons of tree species, differences in characteristics were examined with *t*-tests. We tested for differences among nest trees (DBH and cavity height) for sapsuckers and other woodpecker species using ANOVA, followed by Fisher's Least Significant Difference method ($\alpha = 0.05$) for individual comparisons when the overall ANOVA was significant. All analyses were made using PCSAS on a Windows platform (SAS Inst. 1996). Where ± values are reported, they represent SD.

RESULTS

In the Coram Experimental Forest, nest excavation by Red-naped Sapsuckers began in early to mid-May and young fledged mid-July to early August. We discovered most nests (76%) during the later stage of nestling development, when their vocalizations carry the farthest. Detections probably were biased toward trees with successful nests (Mayfield

TABLE 1. Red-naped Sapsucker nest-tree characteristics, northwestern Montana.

Tree species		DBH (cm)	Tree height (m)	Cavity height (m)	Basal area (m^2/ha)	Canopy cover (%)
Western larch	(n = 84)					
(*Larix occidentalis*)	range	36–119	11.3–50.6	7.9–42.7	0–74	0–100
	$\bar{x}$ (±SD)	69 (20.95)	29.9 (9.12)	21.5 (7.34)	23 (11.54)	33 (15.64)
Paper birch	(n = 30)					
(*Betula papyrifera*)	range	23–58	7.6–18.0	3.0–14.9	0–46	0–50
	$\bar{x}$ (±SD)	37 (8.42)	13.2 (2.68)	9.8 (2.57)	14 (11.62)	23 (15.78)
All others[a]	(n = 11)					
	range	30–81	3.5–36.6	1.4–30.5	5–44	5–50
	$\bar{x}$ (±SD)	45 (15.92)	17.3 (11.11)	12.2 (9.08)	28 (14.67)	34 (19.74)
All nest trees	(n = 125)					
	range	23–119	3.5–50.6	1.4–42.7	0–74	0–100
	$\bar{x}$ (±SD)	59 (23.31)	24.8 (11.09)	17.9 (8.48)	21 (12.44)	30 (16.27)

[a] Four Engelmann spruce (*Picea engelmannii*), two subalpine fir (*Abies lasiocarpa*), one lodgepole pine (*Pinus contorta*), one ponderosa pine (*Pinus ponderosa*), one western hemlock (*Tsuga heterophylla*), one western redcedar (*Thuja plicata*), and one black cottonwood (*Populus trichocarpa*).

1961, Tobalske 1992) and nests closer to the ground, from which vocalizations were most audible.

Nest trees.—We located 125 Red-naped Sapsucker nest trees in old-growth forest. Larch and birch represented 91% of all nest trees, 67% and 24% respectively; seven other tree species made up the remaining 9% (Table 1). Most (68%) nest trees were live and 75% had broken tops (Table 2). External evidence of heartwood decay was present in 87% of larch and 86% of birch. Conks or swollen punk knots were observed on 67% of larch and 66% of birch. All larch (13%) and birch (14%) without specific external evidence of decay had either dead or broken tops. All sapsucker nest excavation chips had visual evidence of decay (e.g., white pockets or bleached areas).

Nineteen of the 30 birch nest trees were within old-growth conifer stands; 11 were remnants in adjacent clearcut old growth. Considering nest trees only in Coram (n = 98), all tree species were not used in proportion to their availability (χ^2 = 1046.45, 3 df, $P < 0.001$). Larch and birch were greatly over utilized whereas Douglas-fir and all other species (grouped) were greatly under utilized (standardized residuals = 18.04, 25.27, −7.14, and −5.60 respectively). We found no significant difference in nest-hole orientation of sapsucker nests (n = 135, χ^2 = 5.740, 7 df, $P > 0.05$).

In addition to sapsuckers, we found five other woodpeckers nesting in old growth: Pileated Woodpecker (*Dryocopus pileatus*), Northern Flicker (*Colaptes auratus*), Hairy Woodpecker (*Picoides villosus*), Three-toed Woodpecker (*P. tridactylis*), and Black-backed Woodpecker (*P. arcticus*). In larch, sapsuckers nested highest and only Pileated

TABLE 2. Red-naped Sapsucker nest-tree conditions based on tree structure and relative amount of dead wood, in northwestern Montana.

	Tree condition					
Nest tree species	Intact-top snag	Broken-top snag	Broken-top live	Dead-top live	Live-top live	Totals
Western larch						
(*Larix occidentalis*)	3	19	38	15	9	84
Paper birch						
(*Betula papyrifera*)	0	11	18	1	0	30
All others[a]	1	6	2	1	1	11
Totals	4	36	58	17	10	125

[a] See Table 1 for list of species.

TABLE 3. Comparison of western larch nest trees used by Red-naped Sapsuckers and other woodpeckers in old-growth forest, northwestern Montana.

Woodpecker species	Larch nest trees		Cavity height (m) Mean ± SD[b]	DBH (cm) Mean ± SD[b]
	n	%[a]		
Red-naped Sapsucker (*Sphyrapicus nuchalis*)	84	67	21.5 ± 7.34 (A)	69 ± 20.95 (A)
Norther Flicker (*Colaptes auratus*)	18	55	18.0 ± 9.64 (A,B)	67 ± 27.09 (A,B)
Pileated Woodpecker[c] (*Dryocopus pileatus*)	52	53	17.5 ± 5.71 (B)	77 ± 14.25 (B)
Hairy Woodpecker (*Picoides villosus*)	15	56	14.7 ± 9.81 (B,C)	41 ± 18.69 (C)
Three-toed Woodpecker (*Picoides tridactylis*)	7	23	8.9 ± 6.55 (C,D)	33 ± 7.59 (C)
Black-backed Woodpecker (*Picoides arcticus*)	5	45	4.7 ± 4.41 (D)	30 ± 13.79 (C)

[a] % of total nest tress that were larch, for each woodpecker species.

[b] Following the SD, the same letter among the species indicates means are not different, based on Fisher's LSD ($\alpha = 0.05$).

[c] See McClelland and McClelland (1999) for a detailed description of Pileated Woodpecker nest and roost trees.

Woodpeckers selected larger diameter nest trees (Table 3).

Reuse of sapsucker nest trees.—About half of the active sapsucker nest trees we checked in successive years ($n = 42$) had an active sapsucker nest both years. Reuse was more common in larch than in birch (62% and 38%, respectively). In 27% of reused trees, the same nest cavity was used (Table 4). Larch nest trees had up to 40 sapsucker nest holes from previous years ($\bar{x} = 4 \pm 5.96$). Birch nest trees had up to 10 additional holes ($\bar{x} = 2 \pm 1.93$). All Mountain Chickadee (*Poecile gambeli*) nests ($n = 36$) were in holes previously excavated by sapsuckers. Most ($n = 33$) were in larch and none was in birch. As expected, Mountain Chickadee larch nest-tree mean DBH (62 ± 23.25 cm) and mean cavity height (20.1 ± 8.07 m) were not different from sapsucker nest trees ($t = 1.62$, 115 df, $P > 0.05$, and $t = 0.94$, 115 df, $P > 0.05$, respectively).

When Red-breasted Nuthatches (*Sitta canadensis*) nested in existing sapsucker cavities (12 of 23 nests), most (11 of 12) were in larch. Nuthatches also excavated original cavities ($n = 11$). When they excavated in larch ($n = 5$), they chose well-decayed trees or snags that were smaller (mean DBH = 41 ± 26.07 cm) than the larch nest trees in which they used abandoned sapsucker cavities (mean DBH = 65 ± 15.64 cm; $t = -2.38$, 14 df, $P < 0.05$). Two Tree Swallow (*Tachycineta bicolor*) nests were in old sapsucker holes, one each in isolated larch and birch. Four cavity nesting species used eight nest trees concurrently with sapsuckers: Mountain Chickadee (5 trees, all in old sapsucker cavities), Chestnut-backed Chickadee (*Poecile rufescens*; 1, in an old sapsucker cavity), Red-breasted Nuthatch (1, in an old sapsucker cavity), and Hairy Woodpecker (1, in a cavity it excavated). Pileated Woodpecker cavities were used by several other birds and small mammals (McClelland and McClelland 1999). One Northern Flicker

TABLE 4. Nest tree and nest cavity reuse by Red-naped Sapsuckers in northwestern Montana. Nest trees ($n = 42$) were observed in two consecutive years.

Nest tree species[a]		No. nest trees not reused	No. nest trees reused		Total no. nest trees reused	%
			Same hole	New hole		
Western larch (*Larix occidentalis*)	($n = 26$)	10	4	12	16/26	(62)
Paper birch (*Betula papyrifera*)	($n = 16$)	10	2	4	6/16	(38)
Totals	($n = 42$)	20	6	16	22/42	(52)

[a] Insufficient data for other species.

nest hole in a birch was used by an American Kestrel (*Falco sparverius*). We detected no subsequent use of Hairy Woodpecker, Three-toed Woodpecker, or Black-backed Woodpecker cavities.

Other secondary cavity nesters.—In contrast to Mountain Chickadees, Black-capped Chickadees (*Poecile atricapillus*) nested only in cavities they excavated in well-decayed trees (*n* = 12; including 7 birch and 2 larch). Their nest trees were isolated or on forest edges, never in the interior of old-growth stands. Nest trees were small (mean DBH = 22 ± 10.27 cm) with cavities low ($\bar{x}$ = 5.0 ± 5.39 m). Black-capped Chickadees exhibited the unique strategy of excavating downward in broken-top birch (*n* = 4), entirely avoiding the bark. In their two larch nest trees, they excavated only 36 cm and 61 cm above the ground at sites with no bark. Each of 10 Brown Creeper (*Certhia americana*) nests was in a snag, in a natural cavity underneath bark that receded from the main stem. Mean DBH of nest trees was 43 ± 18.15 cm and mean cavity height was 6.3 ± 5.06 m. No Brown Creeper nest was in larch; three were in Douglas-fir, three ponderosa pine (*Pinus ponderosa*), two lodgepole pine, one Engelmann spruce, and one subalpine fir.

DISCUSSION

Red-naped Sapsuckers are weak excavators that "can deliver only light blows" (Spring 1965:473). Consequently, they would be expected to select nest trees with soft wood or with wood substantially softened by wood decay. Yellow-bellied Sapsuckers (*Sphyrapicus varius*) in the northeastern United States select aspen infected with *Phellinus igniarius* (Kilham 1971). In Colorado and Wyoming, Crockett and Hadow (1975) found all Red-naped Sapsucker nests (*n* = 51) in aspen, most of which were infected with *P. igniarius*. Daily and coworkers (1993) described the sapsucker as restricted to aspen nesting habitat in Colorado, with nest trees affected by *P. igniarius*. Within a large burn in Glacier National Park, Montana, Caton (1996) found Red-naped Sapsucker nests primarily in aspen (93%). Even undecayed aspen wood is relatively soft [specific gravity = 0.35 (Panshin and deZeeux 1970)] as is the bark, which is easily penetrated. Aspen is not resistant to decay (Manion 1981) and decay produces a central column of softened wood. These factors make aspen a tree easily excavated by sapsuckers.

Unexpectedly, in Montana, Red-naped Sapsuckers were common nesters in old-growth conifer forest, favoring larch and birch. Compared with aspen, larch and birch both are harder [specific gravity of undecayed wood = 0.48 (Panshin and deZeeux 1970)]. Because of the hard wood and tough bark, decay probably is more critical in larch and birch nest trees than in aspen. Birch is not resistant to decay and the inner wood is susceptible to heartrot fungi, especially *Phellinus igniarius* (Bull et al. 1997) and *Fomes fomentarius* (Parks et al. 1997). Although birch bark is durable, it is thin, providing only a brief obstacle to excavation. The remaining bark serves as a shell that surrounds and protects a cavity excavated in the decay-softened wood.

In larch, not only is the wood hard, the sapwood is slower to decay than is the heartwood and the bark is thick. Even the Pileated Woodpecker, a strong excavator, selects larch with heartwood decay (McClelland and McClelland 1999). Sapsuckers apparently avoid the potential impediments in larch by selecting nest trees with extensive heartwood decay and excavating high in the tree. Although larch heartwood is moderately resistant to decay (Manion 1981), it is susceptible to quinine fungus (*Fomitopsis officinalis*) and red ring rot (*Phellinus pini*; Fiedler and Lloyd 1995). Decay of this type develops slowly, over tens or hundreds of years at a rate usually not exceeding 100 cm^3 per year (A. D. Partridge, pers. comm.). Consequently, heartwood decay in larch is significant mainly in old, mature trees (Carlson et al. 1995) with young trees having a low incidence of decay (Boyce 1948, Schmidt et al. 1976, Manion 1981). Although sapsuckers usually nest in relatively small aspen and birch (Table 1), sapsucker selection of large larch was a result of decay related to size and age, not to size itself.

Sapsucker nest cavities in larch were high, usually near a broken top, which is a common point of entry for heartwood decay organisms (Manion 1981). Bark on the lower bole of large larch may be 15 cm thick, but it is much thinner on the upper bole (Schmidt et al. 1976). Sapsuckers excavated progressively lower on the upper bole in succeeding years. The first site selected for excavation may have had most heartwood decay (assuming decay entry through the broken top) combined with thin bark. This contrasts with aspen in which initial sapsucker nest-hole excavations are close to the ground and are progressively higher in ensuing years (Daily 1993). Heartwood decay reportedly invades aspen mostly at the base of the tree (Basham 1958, Shigo 1965).

Because sapsuckers usually make a fresh excavation each year (our data and Lawrence 1967), many nest holes from previous years are available for secondary cavity nesters. Kilham (1971:170) characterized such trees as "tenements." Although Mountain Chickadees and Red-breasted Nuthatches often excavate nest cavities in soft wood (Johnsgard 1986), undecayed larch wood apparently is too hard to penetrate. Their nests in old-growth larch depended on the presence of sapsuckers that in turn depended on the presence of heartwood decay.

Previously, old-growth larch forests have not been considered important habitat for Red-naped Sapsuckers. Our data make evident that in the northern Rocky Mountains, sapsuckers commonly nest in large larch with heartwood decay. Because heartwood decay incidence increases with age, habitat value to Red-naped Sapsuckers and other species is amplified in old growth forests. Consequently, the perpetuation of old-growth western larch forests should be an important component in the conservation of avian diversity.

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SPECIES LIMITS IN PALE-TIPPED TYRANNULETS (*INEZIA*: TYRANNIDAE)

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ABSTRACT.—New information on the vocalizations and behavior of populations of the Pale-tipped Tyrannulet (*Inezia subflava*), along with analysis of biometric and plumage characters, reveal that it actually consists of two species-level groups: a northern/Guianan group, the member taxa of which are weakly differentiated from one another; and a group whose distribution is primarily Amazonian, the member taxa of which are morphologically distinct but vocally and behaviorally similar to one another. The two groups differ from one another in several vocal, plumage, and biometric characters. Tape playback experiments suggest that the vocal differences alone present effective mechanisms for reproductive isolation between the two groups. Analysis of vocalizations further suggests a possible link between the Amazonian representatives of *Inezia subflava* and the Yellow Tyrannulet (*Capsiempis flaveola*). *Received 10 May 1999, accepted 9 Sept. 1999.*

The current taxonomic limits of many Neotropical birds were established by taxonomists who lacked field experience with the birds they were describing. Even the most basic information on vocal characters, behavior, or habitat preference was unknown, and thus, taxa were delimited entirely on the basis of similarities and differences in morphological characters. Consequently, scores of taxa were lumped into wide-ranging polytypic species based solely on shared similarities of plumage (Ridgway 1907, Hellmayr 1927). Modern taxonomists have access to a wealth of behavioral, ecological, vocal, and molecular data on Neotropical birds that was not available to workers just one generation ago. This should allow a more informed classification, and indeed, recent reevaluations of many wide-ranging taxa have resulted in the elevation of many subspecies to full species rank (Pierpont and Fitzpatrick 1983; Willis 1988, 1991; Prum 1994; Bierregaard et al. 1997; Krabbe and Schulenberg 1997; Isler et al. 1997, 1998; Zimmer 1997). Unfortunately, we are still far removed from having a working taxonomy that accurately reflects species-level biodiversity in the Neotropics. Much work remains to be done with respect to reevaluation of species limits in already described polytypic taxa (Prum 1994, Isler et al. 1998, Peterson 1998). Until such work is completed, regional patterns and levels of endemism will continue to be misinterpreted or underestimated, with the result that unique reservoirs of biodiversity could be overlooked when critical conservation decisions are made.

We examine taxonomic limits in one such polytypic species, the Pale-tipped Tyrannulet (*Inezia subflava*). As currently recognized (Sibley and Monroe 1990), *Inezia subflava* ranges widely through the tropical lowlands of eastern Colombia, Venezuela, the Guianas, and Amazonian Brazil to Bolivia (Ridgely and Tudor 1994). Four subspecies were recognized by Traylor (1979): *I. s. subflava, I. s. caudata, I. s. intermedia,* and *I. s. obscura.*

While conducting avifaunal surveys in Amazonas and Roraima, Brazil, we discovered that local populations of Pale-tipped Tyrannulets differed markedly in their vocalizations from populations with which one or the other of us were intimately familiar. Subsequent analysis of specimens and tape recorded vocalizations, together with tape-playback experiments, revealed that *Inezia subflava* consists of two vocally and morphologically distinct species-level groups: a northern/Guianan group consisting of two weakly differentiated subspecies, and an Amazonian group consisting of two morphologically distinct yet vocally similar subspecies.

METHODS

K.J.Z. studied "Pale-tipped" Tyrannulets at various sites in edo. Cojedes, Venezuela (1987–1998) and edo. Amazonas, Venezuela (February–March 1998). Both authors also made numerous observations of these birds along the Rio Juma, Amazonas, Brazil (January

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1993 and 1995); along the Rio Branco near Boa Vista, Roraima, Brazil (November 1994); along the Rio Teles Pires, Mato Grosso, Brazil (September 1997 and 1998); and at multiple sites along the Rio Negro from Manaus to the Anavilhanas Archipelago, Amazonas, Brazil (1991–1998). All behavioral data were summarized verbally on tape in the field, and later transcribed. All measurements used in such data (distances, heights, etc.) are estimates. Mapped distributions (as they appear in this paper) are based on label data from specimens which K.J.Z. examined, and by more recent records documented with tape recordings. These localities, along with the type localities for each taxon, were entered into a geographic information system (Isler 1997) and mapped by M. Isler.

We assume that vocalizations of tyrannulets, like those of other suboscines, are mostly or entirely inherited (Kroodsma 1984, 1989; Kroodsma and Konishi 1991), and consequently provide potentially important characters for systematic study (Lanyon 1978, Willis 1992, Isler et al. 1997, Krabbe and Schulenberg 1997, Zimmer 1997). To analyze vocalizations we assembled recordings of each of the named subspecies of *Inezia subflava*. Locations and recordists for all recordings examined are listed in the Appendix. For comparison, vocalizations were categorized as loudsongs, duet songs, duets, or calls. Loudsongs were consistently patterned multinote vocalizations (Isler et al. 1997) given by an individual bird, seemingly in the context of territorial advertisement. Duet songs were sex-specific multinote vocalizations typically given as part of a duet, but frequently delivered independently as an alternate song type to the loudsong. Duets involved simultaneous delivery of duet songs by both members of a pair. Vocalizations characterized as calls were usually of low amplitude and/or structurally simple (usually involving repetition of identical notes) and were most often given in the context of contact vocalizations between mates. Exceptions are noted in the Results. Our tape recordings were made with Sony TCM-5000 recorders and Sennheiser MKH-70, ME-66, and ME-80 microphones. Spectrograms used in illustrations were made by P. Isler on a Power Macintosh 7500 computer using Canary version 1.2.1 (Bioacoustics Research Program, Cornell Laboratory of Ornithology, Ithaca, New York), Canvas graphics software (version 5.0.3, Deneba Software, Miami, Florida), and a Hewlett Packard Laserjet 6MP printer.

Playback experiments were conducted to determine the reactions of tyrannulets of a given population to vocalizations of another population. In each case, an individual or pair of tyrannulets was first presented with 5–10 tape recordings of one of the other taxa, given at about 15-second intervals. If there was no response, the tyrannulets were then presented with 5–10 tape recordings of their own vocalization type. This was done to account for potential seasonal influences by resolving the question of whether birds that were unresponsive in the first trials were discriminating between the different vocalizations or were generally non-territorial during the trial period and therefore unresponsive to playback of any kind. Failure to account for seasonal differences in responsiveness has been cited as a potential design weakness in other playback experiments (Kroodsma 1986). Responses to playback were characterized as strong, weak, or none. A strong response involved immediate and repeated vocalizations (from previously non-vocalizing birds) as well as approach toward the sound source. A weak response involved single or unsustained vocalizations (from previously non-vocalizing birds) without approach. The none category includes instances in which birds remained silent and did not approach the sound source, as well as instances in which already vocalizing birds neither changed the delivery or pace of their vocalizations nor approached the sound source.

To identify morphological differences, K.J.Z. examined representative specimens of *I. s. subflava* ($n = 31$), *I. s. caudata* ($n = 33$), *I. s. intermedia* ($n = 8$), and *I. s. obscura* ($n = 8$). These specimens are housed at the American Museum of Natural History, New York (AMNH); Carnegie Museum, Pittsburgh (CM); Field Museum of Natural History, Chicago (FMNH); Louisiana State University Museum of Natural Science, Baton Rouge (LSUMZ); Peabody Museum of Natural History, Yale University (YPM); and the Los Angeles County Museum of Natural History, Los Angeles (LACM). A list of the specimens examined is provided in Appendix 2. A wing rule with a perpendicular stop at zero was used to measure flattened wing chord (wing) and tail length (tail), and dial calipers were used to measure tarsus length (tarsus), culmen length from the anterior end of the nares to the tip (culmen), bill depth at the anterior end of the nares (bill depth), and bill width at the anterior end of the nares (bill width). All measurements made with calipers were made to the nearest 0.1 mm; those taken with the wing rule were made to the nearest 0.5 mm. Measurement terminology conforms with that used by Pyle and coworkers (1987).

General linear models were used to investigate gender corrected differences between the four subspecies for each of the six characters measured. Residual diagnostics indicated no violations of the general linear model assumptions of error normality and constant variance. Bonferonni multiple comparisons (two-tailed *t*-test) with a family error rate of 5% were used to compare pairwise subspecies differences for each variable. Bonferonni intervals (Sokal and Rohlf 1995) ensure that the probability of falsely identifying a difference between subspecies when one does not exist remains at most 5% even though multiple comparisons are being made. Intervals that do not contain zero indicate a significant difference among the pair of subspecies. Statistical analyses (ANOVA procedure and Bonferonni multicomp procedure) were performed using S-Plus version 4.5 for Windows.

RESULTS

Distribution.—The type localities of the various subspecies of *Inezia subflava,* along

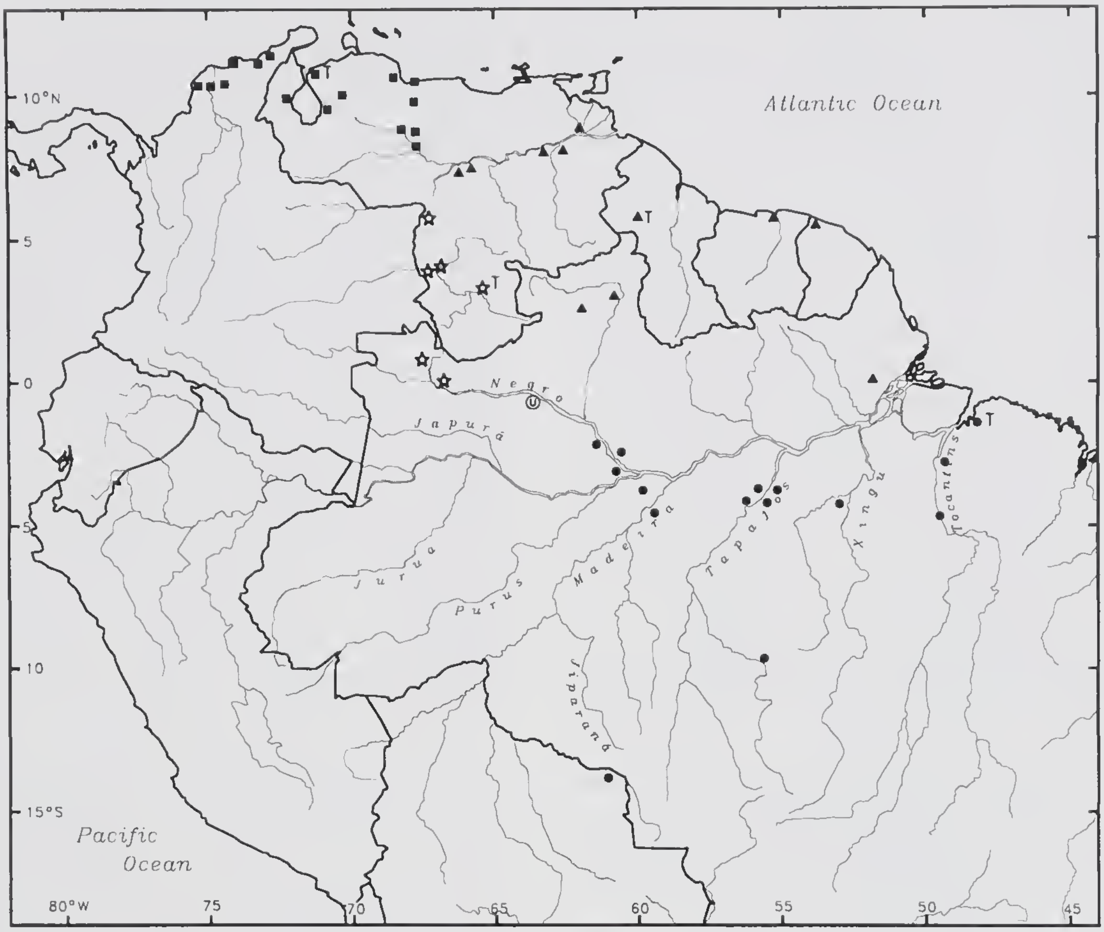

FIG. 1. Distribution of "Pale-tipped" Tyrannulets (*Inezia subflava*) as confirmed by examination of specimens or tape recordings: black squares = *I. s. intermedia*; black triangles = *I. s. caudata*; open stars = *I. s. obscura*; black circles = *I. s. subflava*; "T" next to a symbol indicates the type locality for that taxon and "U" in a circle locates a site near Barcelos, Amazonas, Brazil from which archived tape recordings could not be identified with certainty (either *I. s. obscura* or *I. s. subflava*).

with their distributions as confirmed by specimens or tape recordings examined by K.J.Z. are mapped in Fig. 1. Nominate *I. s. subflava* occurs in southern Amazonian Brazil, from the west bank of the lower Rio Madeira drainage east to the right bank of the Tocantins, and north, locally, along the lower Rio Negro drainage (Peters 1979). It has been found recently to occur south to Alta Floresta in northern Mato Grosso, Brazil (B. Whitney and K. Zimmer, unpubl. data) and locally in depto. Beni and depto. Santa Cruz, Bolivia (Remsen et al 1987; Bates et al. 1989; S. Hilty, pers. comm.). *Inezia s. obscura* is found in southwestern Venezuela in edo. Amazonas (Meyer de Schauensee and Phelps 1978), in adjacent northwestern Brazil in Amazonas (Peters 1979) and in eastern Colombia in depto. Vaupés and depto. Guainía (Hilty and Brown 1986). It probably contacts *I. s. subflava* somewhere along the middle Rio Negro, but this has yet to be determined. *Inezia s. intermedia* is found in northeastern Colombia and eastward locally through much of northern Venezuela north of the Río Orinoco, to edo. Sucre and edo. Monagas (Meyer de Schauensee and Phelps 1978). It is replaced by *I. s. caudata* along both banks of the lower Orinoco from southern edo. Guarico to southern edo. Monagas, and south of the Orinoco in edo. Apure, and in edo. Bolívar along the lower Río Caura (Meyer de Schauensee and Phelps 1978). *Inezia s. caudata* is also found eastward locally through Guyana, Suriname and French Guiana, south to Amapá, Brazil, and in Roraima, Brazil along the northern Rio Branco (Peters 1979, Ridgely and Tudor 1994). Curiously, most of southeastern Venezuela appears to be uninhabited by any form in the complex (S. Hilty, pers. comm.). *Inezia s. caudata* and *I. s. obscura* appear to be parapatric along the Orinoco between southern edo. Apure and northern edo. Amazonas.

Habitat.—All forms of *Inezia subflava* show affinities for wooded areas in the vicinity of water. *Inezia s. intermedia* is particularly common in the seasonally flooded llanos region of Venezuela, where it inhabits the understory and mid-levels of humid gallery forest, as well as lighter deciduous woodland and scrub (K.J.Z., pers. obs.). Similar habitats are occupied in Colombia (Hilty and Brown 1986). *Inezia s. caudata* is found primarily in várzea forest along the Orinoco and various tributaries in Venezuela (Meyer de Schauensee and Phelps 1978; S. Hilty, pers. comm.), but is apparently mostly restricted to mangroves in the Guianan portion of its range (Ridgely and Tudor 1994). *Inezia s. obscura* and *I. s. subflava* are found primarily in the shrubby, water-edge vegetation along forest-bordered rivers, streams, and lakes (K.J.Z. and A.W., pers. obs.). Both forms are locally common in the shrubby borders of seasonally flooded black-water forests (igapó). On river islands in the Rio Negro, nominate birds frequently occupy the thickets bordering central lagoons (K.J.Z. and A.W., pers. obs.).

Behavior.—Little has been recorded of the behavior of Pale-tipped Tyrannulets. In general, all forms occupy the lower to mid-levels of the forest strata, and are usually encountered singly or in pairs independent of mixed-species flocks (Hilty and Brown 1986; K.J.Z. and A.W., pers. obs.). They perch-glean a variety of arthropods from mostly live foliage, while moving with their tail partially cocked (Hilty and Brown 1986; Ridgely and Tudor 1994; K.J.Z. and A.W., pers. obs.). In the Venezuelan llanos, *I. s. intermedia* shows a greater tendency to forage within 2 m of the ground and frequently drops to the ground to glean arthropods from the tops of leaf litter (K.J.Z., pers. obs.). This behavior may be accentuated during the pronounced dry season when most of the trees have dropped all or most of their leaves. At least in this region, *I. s. intermedia* is commonly associated with mixed-species flocks of woodcreepers, Rusty-backed Spinetails (*Cranioleuca vulpina*), other tyrant-flycatchers, and greenlets (K.J.Z., pers. obs.).

Plumage.—The four subspecies of Pale-tipped Tyrannulet are so similar in plumage characters that silent birds could defy identification in the field. In direct comparison, specimens are readily separable into two groups based on ventral coloration. *Inezia s. caudata* and *I. s. intermedia* are tinged buffy or ochraceous on the throat and breast, contrasting with a whitish chin and a clearer yellow belly and vent. This ochraceous coloring is strongest in *I. s. caudata,* whereas *I. s. intermedia* has a paler throat and less ochraceous on the breast. Both *I. s. subflava* and *I. s. obscura* lack any buffy or ochraceous tones to the underparts, are more saturated with yellow on the chin and throat, and are flammulated olivaceous on the sides of the breast. *Inezia s. obscura* is strongly washed olivaceous across the center of the breast, making the throat appear contrastingly brighter yellow, whereas the median underparts of *I. s. subflava* are yellow from the chin down. *Inezia s. caudata* and *I. s. intermedia* have slight contrast between the grayish crown and the olive-brown back, whereas *I. s. subflava* and *I. s. obscura* are more uniformly olivaceous above. All forms have the wings and tail dusky, with two whitish wingbars, pale edges to the outer vanes of the rectrices, and the rectrices tipped pale buffy-white. Field work suggests that there may be consistent differences in iris color, with *I. s. intermedia* having conspicuously pale (whitish or yellowish-white) irides, whereas those of *I. s. subflava* and *I. s. obscura* are brownish. We have not been able to ascertain the eye color of *I. s. caudata.*

Size.—Subspecies of *Inezia subflava* differed significantly from one another in mean measurements of several characters (Tables 1, 2; Fig. 2). Significant between-taxa differences were found in measurements of culmen ($F_{3,74} = 40.4$, $P < 0.001$), bill depth ($F_{3,74} = 12.0$, $P < 0.001$), bill width ($F_{3,74} = 12.2$, $P < 0.001$), wing chord ($F_{3,74} = 6.0$, $P < 0.001$), and tarsus ($F_{3,74} = 16.9$, $P < 0.001$). *Inezia s. caudata* and *I. s. intermedia* differed from one another only in culmen length ($t = 2.96$, df = 74, $P < 0.005$) and bill width ($t = 2.78$, df = 74, $P < 0.01$). *Inezia s. caudata* and *I. s. obscura* differed in culmen length ($t = -8.93$, df = 74, $P < 0.001$), bill depth ($t = -4.45$, df = 74, $P < 0.001$), bill width ($t = -4.16$, df = 74, $P < 0.001$), and tarsus length ($t = 4.88$, df = 74, $P < 0.001$). Nominate *I. s. subflava* and *I. s. caudata* differed in culmen length ($t = -4.12$, df = 74, $P < 0.001$) and tarsus length ($t = 5.89$, df = 74, $P < 0.001$). *Inezia s. intermedia* and *I. s. subflava* differed

TABLE 1. Means (± SD) and ranges of selected measurements (mm) of the four subspecies of Pale-tipped Tyrannulet (*Inezia subflava*). Significance: * = $P < 0.001$; ** = $P < 0.0001$. Values of F and P (= probability of a greater value of F) derived from Analysis of Variance (ANOVA). Asterisks following a character indicate significant differences between two or more of the subspecies, after correcting for potential sex differences within taxa.

Characters	*caudata* $n = 33$	*intermedia* $n = 8$	*subflava* $n = 31$	*obscura* $n = 8$	F
Culmen**	6.3 ± 0.3	6.0 ± 0.3	6.6 ± 0.3	7.4 ± 0.3	40.4
	5.5–7.0	5.6–6.3	6.2–7.3	7.0–8.0	
Bill depth**	3.1 ± 0.2	2.9 ± 0.2	3.1 ± 0.2	3.5 ± 0.1	12.0
	2.5–3.5	2.5–3.1	2.6–3.5	3.3–3.6	
Bill width**	3.6 ± 0.3	3.3 ± 0.3	3.5 ± 0.3	4.1 ± 0.2	12.2
	3.0–4.3	2.7–3.8	2.9–4.4	3.7–4.4	
Wing chord*	49.5 ± 2.2	50.4 ± 2.0	48.2 ± 1.5	50.3 ± 1.9	6.0
	45–53.5	48–52.5	46–51	48–53	
Tail	50.0 ± 2.6	51.2 ± 1.6	49.0 ± 2.4	50.6 ± 1.9	2.6
	44–54	49–53	44–53	48–53.5	
Tarsus**	16.5 ± 0.9	16.3 ± 0.8	15.3 ± 0.6	15.0 ± 0.5	16.9
	14.2–18.3	15.1–17.3	14.4–16.6	14.2–15.8	

in culmen length ($t = -5.52$, df = 74, $P < 0.001$), bill depth ($t = -2.84$, df = 74, $P < 0.01$), wing chord ($t = 2.71$, df = 74, $P < 0.01$), and tarsus length ($t = 3.08$, df = 74, $P < 0.01$). *Inezia s. intermedia* and *I. s. obscura* differed in culmen length ($t = -9.29$, df = 74, $P < 0.001$), bill depth ($t = -5.83$, df = 74, $P < 0.001$), bill width ($t = -5.39$, df = 74, $P < 0.001$), and tarsus length ($t = 3.32$, df = 74, $P < 0.01$). Nominate *I. s. subflava* and *I. s. obscura* differed in culmen length ($t = 6.26$, df = 74, $P < 0.001$), bill depth ($t = 4.02$, df = 74, $P < 0.001$), bill width ($t = 4.79$, df = 74, $P < 0.001$), and wing chord ($t = 2.77$, df = 74, $P < 0.01$). The two southern subspecies (*I. s. subflava* and *I. s. obscura*) were larger billed and shorter legged than the two northern subspecies (*I. s. intermedia* and *I. s. caudata*). *Inezia s. obscura* was the largest billed and shortest legged of the four taxa, whereas *I. s. intermedia* was the smallest billed and longest winged.

Vocalizations.—We assembled 96 separate recordings containing more than 600 individual songs, duets, or calls. Analysis of vocalizations reveals that the four taxa separate into two distinct groups. The loudsong of *I. s. intermedia* (Fig. 3A, B) is a short series of notes in which the first 1–2 notes are louder and slightly separated from the rest (*cheep cheedeleet*). It is often preceded by several irregularly spaced single-note *pip* or *kep* calls (second song in Fig. 3A). This is the most frequently heard vocalization from *I. s. inter-*

TABLE 2. Results of Bonferroni multiple comparisons of five biometric variables (culmen, bill depth, bill width, wing chord and tarsus length) between the four subspecies of Pale-tipped Tyrannulet (*Inezia subflava*). A sixth variable (tail length) showed no significant differences in any of the comparisons, and is excluded from this table. Codes for the taxa are as follows: caud = *I. s. caudata*; inter = *I. s. intermedia*; obsc = *I. s. obscura*; and subfl = *I. s. subflava*. Degrees of freedom for all t-values = 74. Differences between taxa are considered significant only when $P < 0.0083$, to achieve a Bonferroni family error rate of 0.05.

	Culmen		Bill depth		Bill width		Wing		Tarsus	
	t	P	t	P	t	P	t	P	t	P
caud-inter	2.96	0.004	2.48	ns	2.78	0.007	−1.01	>0.05	0.62	>0.05
caud-obsc	−8.93	<0.001	−4.45	<0.001	−4.16	<0.001	−1.01	>0.05	4.88	<0.001
caud-subfl	−4.12	<0.001	−0.58	>0.05	1.13	>0.05	1.62	>0.05	5.89	<0.001
inter-obsc	−9.29	<0.001	−5.38	<0.001	−5.39	<0.001	−0.01	>0.05	3.32	0.001
inter-subfl	−5.52	<0.001	−2.84	0.006	−2.05	>0.05	2.71	0.008	3.08	0.003
obsc-subfl	6.26	<0.001	4.02	<0.001	4.79	<0.001	2.77	0.007	−1.18	>0.05

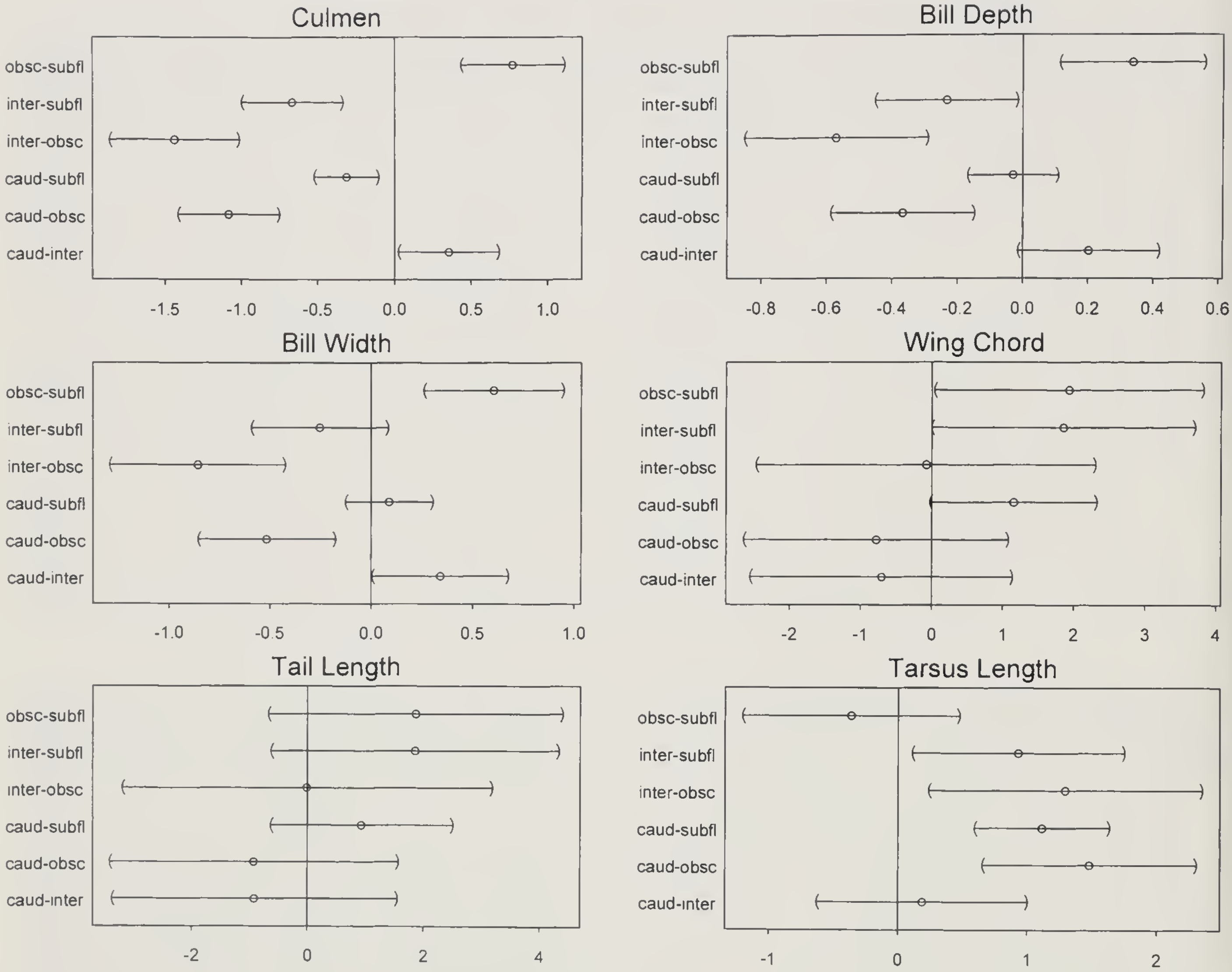

FIG. 2. Graphical display of Bonferonni multiple comparisons of six biometric variables (culmen, bill depth, bill width, wing chord, tail length, and tarsus length) between the four subspecies of Pale-tipped Tyrannulet (*Inezia subflava*; two-tailed *t*-test, df = 74). Test values are found in Table 2. Codes for the taxa are as follows: obsc = *I. s. obscura*, subfl = *I. s. subflava*, inter = *I. s. intermedia*, and caud = *I. s. caudata*. Intervals that do not contain zero indicate a significant difference among the pair of subspecies being compared.

media and is given throughout the day (K.J.Z., pers. obs.). The loudsong of *I. s. candata* (Fig. 3C) is similar in pattern, number of notes, frequency range, and shape of some of the individual notes. The similarities between loudsongs of the two taxa are even more pronounced to the human ear than the spectrograms would suggest. *Inezia s. intermedia* has an alternate song (Fig. 3D) that is a loud, descending series of about 8–15 evenly spaced notes (*chee, cheep cheep cheep cheep chew chew chew*), in which the first note is slightly separated from the rest. A version of this song is given by both sexes during duets (Fig. 3E). The pattern, number of notes, and pitch of these respective male and female duet songs are similar, although they differ in tonal quality and inflection. One or two loud notes from one member of the pair is often the synchronizing cue for the partner to join in. Duet songs may be delivered in an antiphonal manner such that the notes of the male's song alternate with those of the female, or they may be delivered in nearly perfect synchrony. These songs are frequently given by a single bird outside of a duet context, particularly in response to tape playback of the loudsong. Our small sample of *I. s. caudata* vocalizations does not include duets or alternative songs. The dawn song (Fig. 3F) of *I. s. intermedia* is similar to its loudsong, but is faster and repeated at about 1 s intervals for several minutes. Two additional types of calls are regularly given by *I. s. intermedia*. The first is a loud *chew* note that may be given singly (Fig. 3G) or in a series of 5–15 well-spaced (1 note/

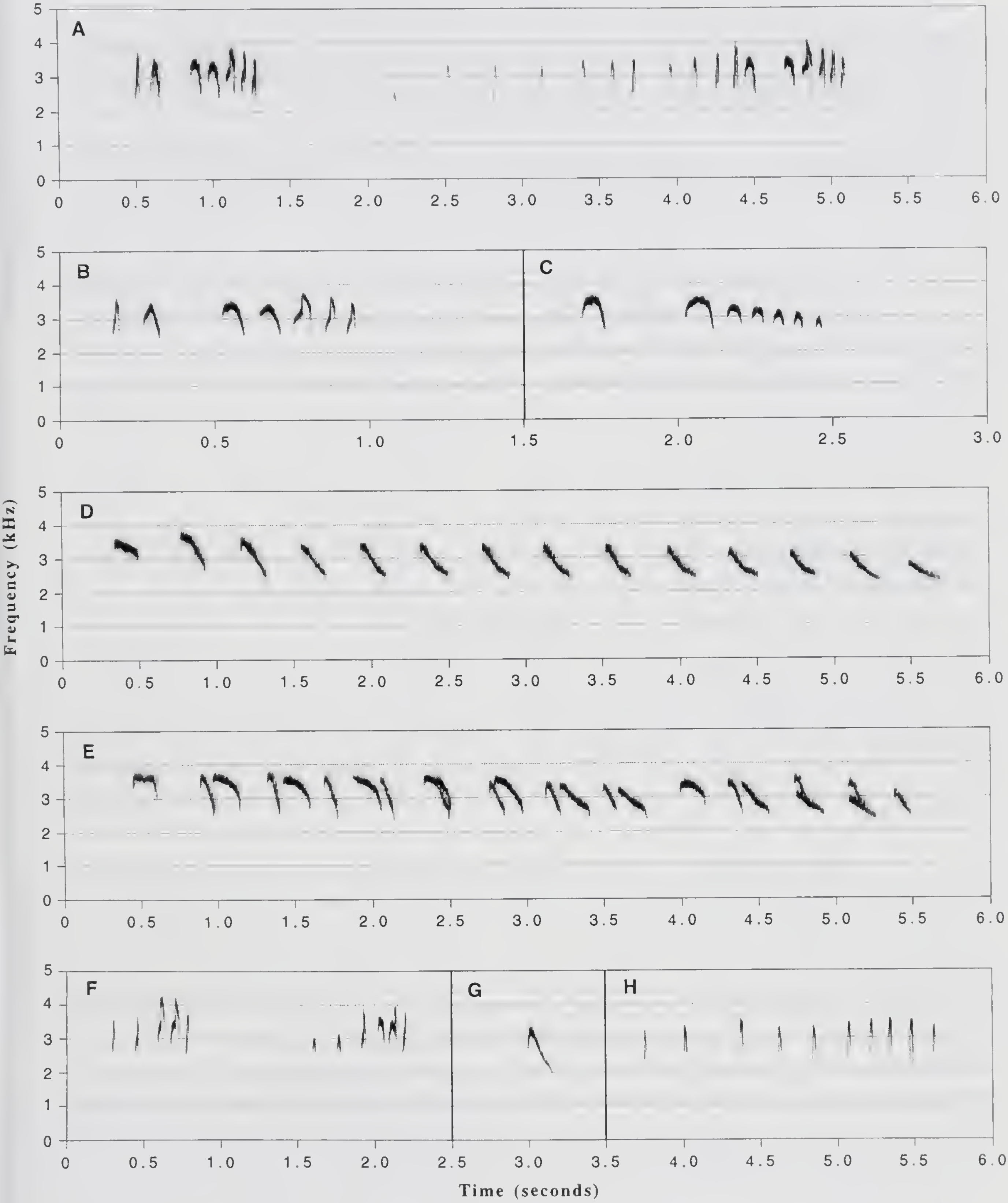

FIG. 3. Types of vocalizations of *Inezia subflava intermedia* and *I. s. caudata*: (A) two loudsongs of *I. s. intermedia* from edo. Cojedes, Venezuela (K. J. Zimmer recording); (B) first song of 3A magnified 200% on the time axis; (C) loudsong of *I. s. caudata* (same scale as 3B) from Suriname (M. and P. Isler recording, LNS #26586); (D) alternate or duet call of *I. s. intermedia* from edo. Cojedes, Venezuela (T. A. Parker recording, LNS #45560); (E) duet of *I. s. intermedia* from edo. Cojedes, Venezuela (T. A. Parker recording, LNS #45560); (F) dawn song of *I. s. intermedia* from edo. Guarico, Venezuela (P. Schwartz recording, LNS #66629); (G) *pew* call of *I. s. intermedia* from edo. Cojedes, Venezuela (K. J. Zimmer recording); (H) *pit* call of *I. s. intermedia* from edo. Cojedes, Venezuela (K. J. Zimmer recording).

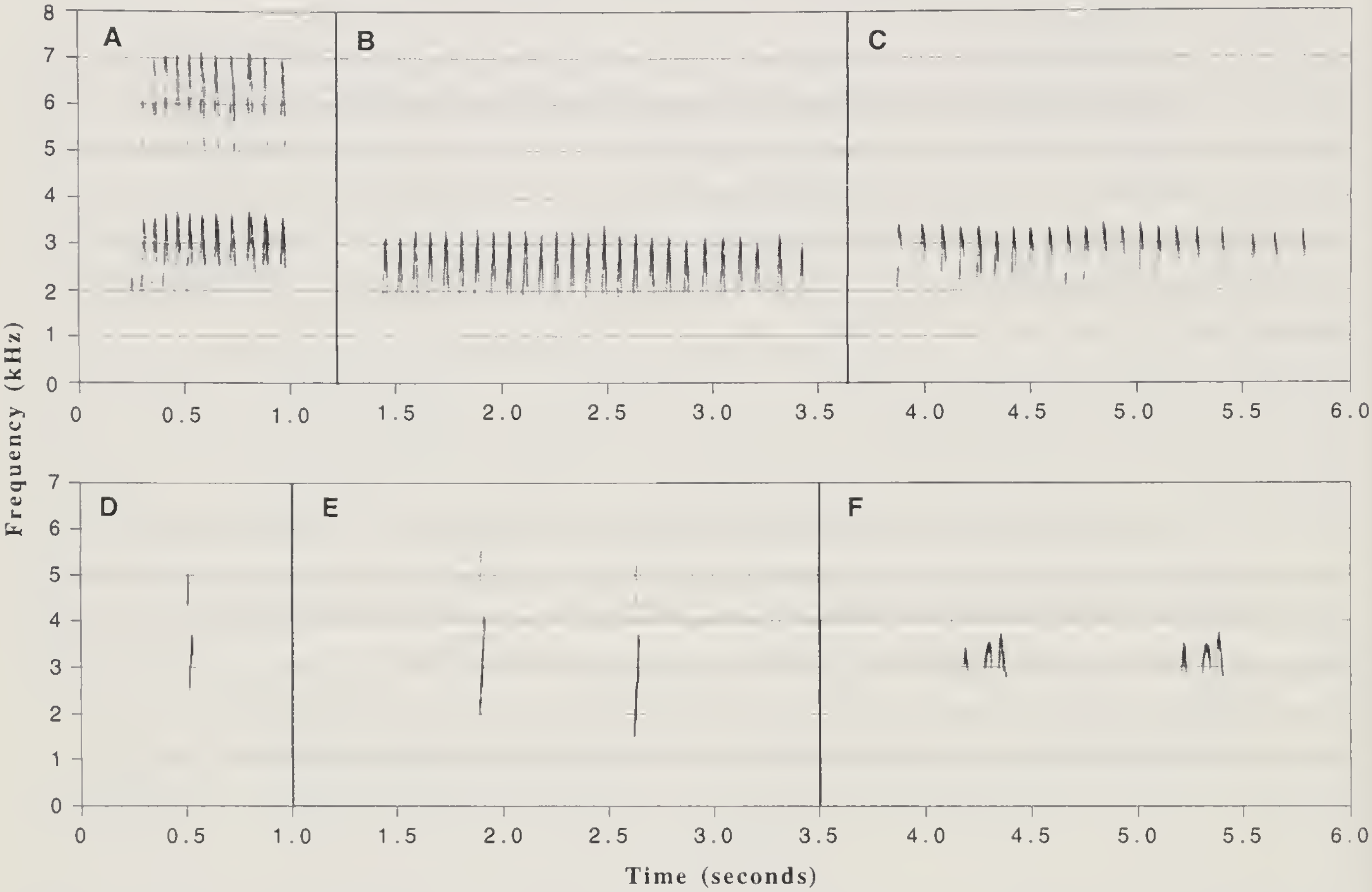

FIG. 4. Types of vocalizations of *Inezia subflava*: (A) loudsong of *I. s. obscura* from São Gabriel da Cachoeira, Amazonas, Brazil (B. M. Whitney recording); (B) loudsong of *I. s. subflava* from Alta Floresta, Mato Grosso, Brazil (B. M. Whitney recording); (C) rattle of *I. s. intermedia* in response to tape playback, from edo. Cojedes, Venezuela (K. J. Zimmer recording); (D) *pik* call of *I. s. subflava* from Rio Juma, Amazonas, Brazil (K. J. Zimmer recording); (E) *pik* calls of *I. s. obscura* from São Gabriel da Cachoeira, Amazonas, Brazil (B. M. Whitney recording); and (F) *teedlee* calls of *I. s. obscura* from edo. Amazonas, Venezuela (K. J. Zimmer recording).

1.5–2 s) notes. This call is frequently given by birds responding to playback. The most common call is an abbreviated *pit* note, which may be given singly, or, more commonly, in an irregularly spaced series of several notes (Fig. 3H). These *pit* calls are typically given as contact notes between mates or family members, and often serve as a prelude to duets.

What we consider the loudsong of both *I. s. obscura* and *I. s. subflava* is a dry rattle on one pitch, formed by a series of closely spaced, identical notes, delivered at about 2–3.5 kHz and lasting 0.5–2.0 s (Fig. 4A, B). These rattles are given at regular intervals throughout the day by individual birds in the absence of playback. The only similar vocalization that we have ever heard from *I. s. intermedia* or *I. s. caudata* was a single sputtering rattle given by a highly agitated *I. s. intermedia* in response to playback (Fig. 4C). This represented a single occurrence in over 400 field hours with *I. s. intermedia* and no similar vocalization is present on any of the tape recordings from other recordists in our inventory. Thus, we believe that rattles are rarely used components of the vocal repertoires of those forms.

Both *I. s. subflava* and *I. s. obscura* routinely give abrupt *pik* notes (Fig. 4D, E) that are analogous to the *pit* calls of *I. s. intermedia* (Fig. 3H), but which are higher pitched. These calls are typically given as contact calls between mates. K.J.Z. has recorded a somewhat musical *teedlee* call (Fig. 4F) from *I. s. obscura*. This call seems to be given rarely, and we are uncertain of the context. We have not recorded a similar call from *I. s. subflava*.

Both sexes of *I. s. obscura* and *I. s. subflava* have an alternate song that is most frequently given as part of a duet. What we believe to be the male duet song in both forms is an

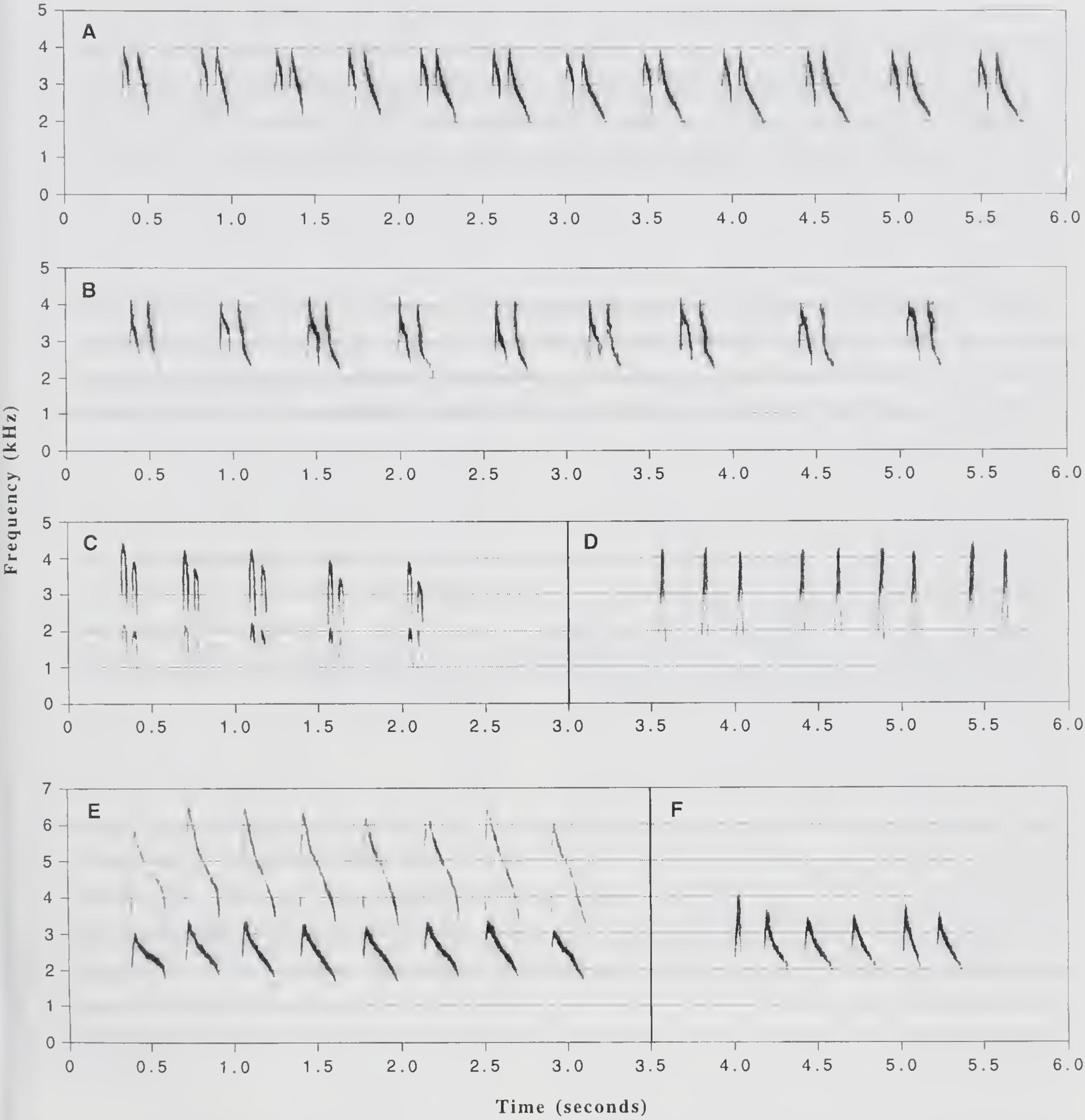

FIG. 5. Types of vocalizations of *Inezia subflava obscura* and *I. s. subflava*: (A) *pee-chew* duet songs (presumed male) of *I. s. obscura* from São Gabriel da Cachoeira, Amazonas, Brazil (B. M. Whitney recording); (B) *pee-chew* duet songs (presumed male) of *I. s. obscura* from edo. Amazonas, Venezuela (K. J. Zimmer recording); (C) *kutup* duet songs (presumed female) from edo. Amazonas, Venezuela (K. J. Zimmer recording); (D) *kip* calls of *I. s. subflava* from depto. Santa Cruz, Bolivia (S. L. Hilty recording); (E) response calls of *I. s. subflava* from Amazonas, Brazil (A. Whittaker recording); and (F) response calls of *I. s. obscura* from edo. Amazonas, Venezuela (K. J. Zimmer recording).

explosive series of evenly pitched *pee-chew* couplets, delivered at about 2/s (Fig. 5A, B). What we believe to be the female duet song in both forms is a lower amplitude series of bisyllabic *kutup* or trisyllabic *kutterup* calls, delivered slightly faster (Fig. 5C). Because these tyrannulets are sexually monomorphic, it was not possible (in the absence of hand-sexed, color-marked birds) to assign a particular vocalization to one sex with absolute certainty. However, birds of both forms which gave the louder *pee-chew* series were also consistently the first members of a pair to respond aggressively to tape playback. These *pee-chew* songs were more frequently delivered independent of a duet. Within duets by mated pairs, one individual consistently gave the *pee-chew* series, whereas the other individual consistently gave the *krurp* or *krrterup* song. Thus, we assume that the different types of alternate songs are specific to one sex or the other. The louder amplitude of the *pee-chew* songs, along with their greater frequency of occurrence outside of duets, and the more aggressive territorial response of individuals which gave them point to these being male songs.

Duets of *I. s. subflava* (Fig. 6A–C) and *I. s. obscura* (Fig. 6D, E) were similar to one another, but differed markedly from those of *I. s. intermedia* (Fig. 3E). One or more *pik* notes delivered by each member of a pair was most often the synchronizing cue for one of the birds (usually the one giving the *pee-chew* calls, and thus, the presumed male) to begin its duet song, with the mate immediately chiming in with its duet song. The male and female duet songs were then delivered simultaneously, creating a jumbled, rollicking effect that was distinctly different from the measured, penetrating duets of *I. s. intermedia.* Less frequently, one member of a pair would give 5–10 emphatic *kip* notes (Fig. 5D) to initiate a duet (Fig. 6C). Duets varied in length and pace between and within pairs. Pairs that were particularly agitated by playback frequently sang at a faster pace and gave more prolonged duets.

An additional vocalization given by both *I. s. subflava* and *I. s. obscura* is a loud series of five or more *chew* notes delivered at about 3 notes/s and usually preceded by a differentiated first note (as in *pee chew chew chew chew chew*; Fig. 5E, F). We call this the response call because it was typically given only in response to tape playback. Birds of both sexes gave this call. These calls were similar in quality to the *chew* call of *I. s. intermedia,* but were always given in a series and much faster.

In both their rollicking, jumbled duets and their rattled loudsongs, *I. s. subflava* and *I. s. obscura* are far more similar vocally to the Yellow Tyrannulet (*Capsiempis flaveola*; Fig. 7) than either is to *I. s. intermedia* or *I. s. caudata.*

Playback experiments.—K.J.Z. conducted playback experiments in edo. Cojedes, Venezuela in February 1995, 1997, and 1998; in edo. Amazonas, Venezuela in February 1998; and in Mato Grosso, Brazil in September 1998. In the 1995 and 1997 trials, individuals or pairs of *I. s. intermedia* were presented with tape recordings of *I. s. subflava* from the Rio Juma (a west-bank tributary of the Rio Madeira, south of the Amazon), Amazonas, Brazil. There was no response to these recordings from any of the 28 pairs or individuals tested. When presented with recordings of *I. s. intermedia,* tyrannulets in all 28 territories responded strongly. In 1998, individuals or pairs of *I. s. intermedia* from 15 territories were presented with recordings of *I. s. obscura* from São Gabriel da Cachoeira, Amazonas, Brazil. None of the 15 pairs responded. When presented with recordings of their own vocal type, all birds responded strongly.

In the other February 1998 trials, individuals or pairs of *I. s. obscura* at three different sites in edo. Amazonas, Venezuela (Yapacana National Park, San Fernando de Atabapo, and Puerto Ayacucho) were presented with a recording of *I. s. subflava* from the Rio Juma, Amazonas, Brazil. Tyrannulets from each of the 11 territories we sampled responded strongly to tape playbacks of nominate birds. In September 1998, a pair of *I. s. subflava* near Alta Floresta, Mato Grosso, Brazil was first presented with tape of *I. s. caudata* from Suriname. The birds did not respond to these playbacks. We then switched to a tape of *I. s. obscura* from edo. Amazonas, Venezuela and the birds responded with an immediate approach and duet.

DISCUSSION

Analysis of vocal characters links *I. s. subflava* with *I. s. obscura.* The two forms have similar loudsongs, male and female duet songs, duets, and calls. Based on current sample sizes of tape recorded vocalizations, we are unable to diagnosably differentiate vocalizations of the two subspecies. *Inezia s. intermedia* differs markedly from the *subflava-obscura* group in its loudsong, male and female duet songs, duets and some calls. Neither our inventory of tape recordings nor our limited field experience with *I. s. caudata* allows a comparison of duet songs or duets of that form with any of the other subspecies. How-

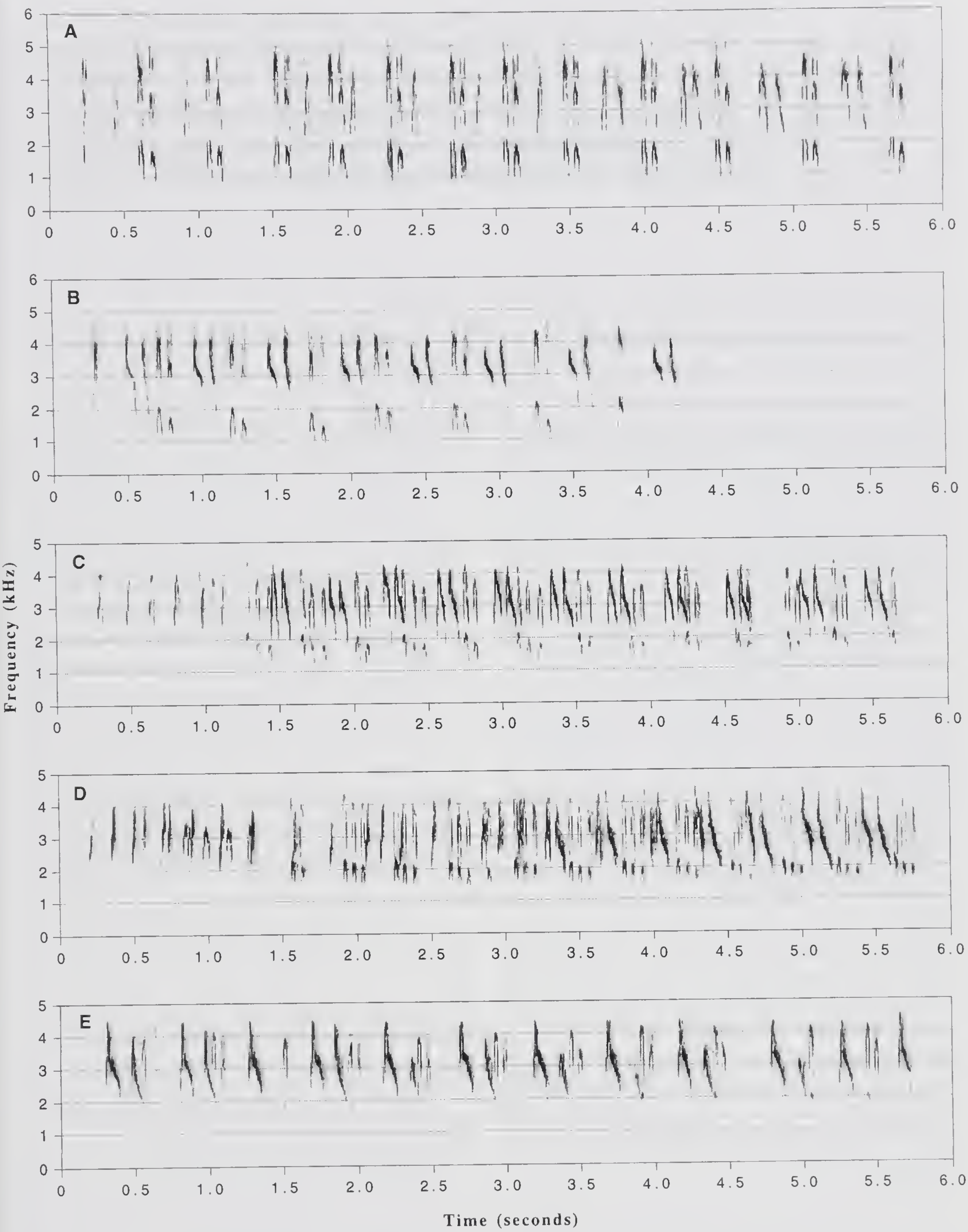

FIG. 6. Duets of *Inezia subflava subflava* and *I. s. obscura*: (A) *I. s. subflava* from Ziggylandia, Amazonas, Brazil (A. Whittaker recording); (B) *I. s. subflava* from depto. Santa Cruz, Bolivia (S. L. Hilty recording); (C) *I. s. subflava* from Alta Floresta, Mato Grosso, Brazil (B. M. Whitney recording); (D) *I. s. obscura* from Yapacana National Park, edo. Amazonas, Venezuela (K. J. Zimmer recording); and (E) *I. s. obscura* from Pto. Ayacucho, edo. Amazonas, Venezuela (K. J. Zimmer recording).

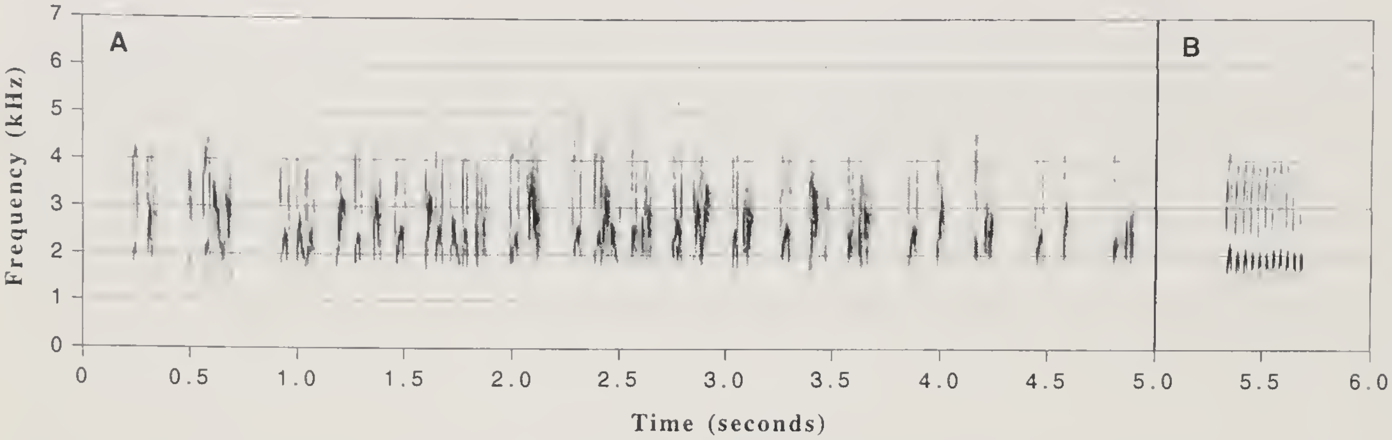

FIG. 7. Vocalizations of Yellow Tyrannulet (*Capsiempis flaveola*) from Pto. Ayacucho, edo. Amazonas, Venezuela: (A) duet; (B) loudsong (K. J. Zimmer recordings).

ever, *I. s. caudata* is similar to *I. s. intermedia* in both its loudsongs and *pit* calls, and is therefore strongly differentiated from the *subflava-obscura* group. We expect that further work will reveal that *I. s. caudata* has duet songs and duets similar to those of *I. s. intermedia.*

Pairings of taxa based on vocal differences are supported by the results of tape playback experiments. Although we were unable to conduct all possible pairwise tests, the ones performed were unequivocal. *Inezia s. intermedia* did not react to playback of either *I. s. subflava* or *I. s. obscura* in any of the 43 trials conducted. Pairs of *I. s. obscura* responded strongly to playback of nominate *I. s. subflava* vocalizations in each of 11 trials. The lone pair of *I. s. subflava* tested did not respond to playback of *I. s. caudata,* but responded strongly to vocalizations of *I. s. obscura.* These trials demonstrate that *I. s. obscura* and *I. s. subflava* recognize and respond strongly to one another's voices, whereas *I. s. intermedia* responds to neither. The lack of response of nominate *I. s. subflava* to playback of *I. s. caudata* songs suggests that *I. s. subflava* would be similarly unresponsive to playback of the nearly identical sounding *I. s. intermedia.*

Morphological differences within the complex correspond to the divisions suggested by vocal characters. *Inezia s. intermedia* and *I. s. caudata* are weakly differentiated from one another. Of six mensural characters we examined, the two forms differed only in culmen length and bill width. Both forms differed from *I. s. obscura* by four characters (culmen length, bill depth, bill width, and tarsus length) and from *I. s. subflava* by culmen length and tarsus length (*I. s. intermedia* further differed from nominate *I. s. subflava* by bill depth and wing chord.). Despite the pronounced vocal similarities between them, *I. s. subflava* and *I. s. obscura* were as biometrically different from one another as either was from *I. s. intermedia* or *I. s. caudata.*

Differences in plumage characters, although subtle, also correspond with the vocal differences. *Inezia s. intermedia* and *I. s. caudata* are distinguished from the other two subspecies in having a buffy or ochraceous wash to the breast, a whiter chin, and a somewhat grayer crown. *Inezia s. subflava* and *I. s. obscura* are united by their brighter yellow throat and breast (with no buffy or ochraceous tones), olivaceous sides of the breast, and more uniformly olivaceous upperparts. This agrees with Hellmayr (1927:389), who stated that *I. s. subflava* "closely resembles the better known *I. s. caudata* from Venezuela and Guiana, but differs principally by more olivaceous (less brownish) upper parts, without any grayish suffusion on forehead; more yellowish sides of the head; less white on chin, and deeper yellow under parts, without buffy tinge on throat and foreneck."

In plumage, as in biometrics, *I. s. intermedia* and *I. s. caudata* are only weakly differentiated. Hellmayr (1927:390) described *I. s. intermedia* as "very similar to *I. s. caudata,* but slightly more olivaceous above; wing bands more whitish; under parts brighter as well as more uniform yellow, with the buffy tinge on the chest barely suggested." He also noted that upperpart coloration in *I. s. caudata* was "rather variable", that "the amount of buffy suffusion below is also subject to considerable variation", and that some specimens from Venezuela "closely approach the western race *intermedia* by having very little buffy on the foreneck." Our examination of specimens did not suggest any consistent plumage differences between the two forms except for a paler chin in *I. s. intermedia* and a buffier breast in *I. s. caudata.*

Differences in iris color could prove to be the most obvious morphological character separating the two groups. Iris color as we have observed it in the field is whitish or pale yellowish for *I. s. intermedia* and brownish for *I. s. subflava* and *I. s. obscura.* This agrees with Ridgely and Tudor (1994:470), who state that iris color "seems consistently yellow in n. Colombia and n. Venezuela, dark in s. Venezuela and the Guianas." This statement suggests that *I. s. caudata* (the Guianan form) is dark-eyed, which, if correct, would be the most conspicuous morphological character separating that form from *I. s. intermedia.* Ridgely and Tudor (1994) also raise the possibility that observed variation in eye color is age related, with younger birds having dark eyes. This seems unlikely given that we have noted territorial pairs of *I. s. obscura* and *I. s. subflava* with brownish eyes, although this does not preclude the possibility that juveniles of *I. s. intermedia* are also dark-eyed. We need confirmation that perceived differences in iris color are consistent for all members of each form.

The vocal similarities between "Pale-tipped Tyrannulets" of the *subflava-obscura* group and *Capsiempis* are intriguing. Like *I. s. subflava* and *I. s. obscura, Capsiempis* is a small, foliage-gleaning tyrannid that occupies shrubby forest borders and second-growth (often lightgaps within forest), as well as open várzea and bamboo (Hilty and Brown 1986; Ridgely and Tudor 1994; K.J.Z. and A.W., pers. obs.). *Capsiempis* is currently considered a monotypic genus whose affinities have been debated. Traylor (1977) subsumed it with *Phylloscartes,* whereas Lanyon (1984) argued that on the basis of nasal septum and syringeal morphology it was closer to *Phaeomyias.* The monophyly of *Inezia* has also been debated (Lanyon 1988), spurred largely by heterogeneity of external morphology in the group. Both genera are considered part of the Tyrannidae subfamily Elaeniinae. To our knowledge, vocal characters have not been given weight in the debates regarding either the monophyly of *Inezia* or the relationships of *Capsiempis,* but perhaps they should. Vocal similarities between *Capsiempis* and *I. s. subflava* and *I. s. obscura* are stronger than between any of the other species currently placed in *Inezia* (K.J.Z. and A.W., pers. obs.).

More field work is needed to ascertain the location and nature of possible contact zones between *I. s. subflava* and *I. s. obscura* in the middle Rio Negro drainage; between either of those forms and *I. s. caudata* along the lower Rio Branco; between *I. s. obscura* and *I. s. caudata* in edo. Apure and edo. Amazonas, Venezuela; and between *I. s. intermedia* and *I. s. caudata* along the north bank of the middle and lower Orinoco. In particular, more field work with *I. s. caudata* is needed to clarify the extent of vocal differentiation from *I. s. intermedia,* as well as the question of possible differences in iris color.

TAXONOMIC CONCLUSIONS

Inezia subflava subflava and *I. s. obscura* differ substantially from *I. s. intermedia* and *I. s. caudata* in multiple vocal and morphological characters. The magnitude of these differences is more than sufficient to support the recognition of the two groups as separate species under any of the widely accepted species concepts (McKitrick and Zink 1988). Because the two groups of taxa are allopatrically distributed, the most difficult species concept to satisfy is the biological species concept. A primary challenge in applying the biological species concept to allopatrically distributed taxa is the need to judge whether or not the taxa are sufficiently differentiated as to prevent extensive hybridization in the event of secondary contact. Carefully designed playback experiments can provide convincing evidence of whether vocal differentiation confirmed by spectrographic analysis is a sufficient barrier to interbreeding. In the *Inezia subflava* complex tape playback experiments suggest that the vocal differences alone present effective mechanisms for reproductive isolation between the two groups. Thus, we propose that the complex consists of two polytypic biological species as follows:

Inezia subflava Sclater and Salvin—Amazonian Inezia
  I. s. subflava Sclater and Salvin
  I. s. obscura Zimmer
Inezia caudata Salvin—Pale-tipped Inezia
  I. c. caudata Salvin
  I. c. intermedia Cory

The two forms of *I. subflava* are united by vocal characters, but are well differentiated on the basis of plumage and biometrics. The two forms of *I. caudata* appear to be weakly differentiated. The existence of morphologically intermediate specimens from the vicinity of the Río Orinoco suggests that *I. c. caudata* and *I. c. intermedia* intergrade in central Venezuela, and that morphological variation between the two forms could be clinal. In the absence of more complete vocal data for *I. c. caudata,* we will continue to recognize *I. c. intermedia* as a distinct taxon.

We advocate a return to the use of "Inezia" in the English names of these birds. Such usage will serve to distinguish this small genus (four species now recognized) from the myriads of other "tyrannulets." With respect to modifiers, we suggest the application of "Amazonian Inezia" to *I. subflava,* which is the only species in the genus with an essentially Amazonian distribution. "Pale-tipped Inezia" offers a link with the former name of Pale-tipped Tyrannulet, and we feel that it should be applied to the two forms of *I. caudata,* which are the most familiar members of the complex to most biologists and birders.

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APPENDIX 1

Recording locations and recordists. Numbers following each name represent the number of recordings from the recordist at each site.

Inezia s. intermedia.—VENEZUELA: Hato Piñero, edo. Cojedes (T. A. Parker 1, K. J. Zimmer 36); Hato El Milagro, edo. Cojedes (P. Schwartz 4); Hato Corozal, edo. Barinas (P. Schwartz 1); Hato Flores Morades, edo. Guarico (P. Schwartz 6); Hato la Trinidad, edo. Guarico (P. Schwartz 2); Hato Masaquaral, edo. Guarico (P. Schwartz 1); Pie de Cuesta, edo. Lara (P. Schwartz 1); Cañada el Gordo, edo. Zulia (P. Schwartz 1).

Inezia s. caudata.—BRAZIL: Boa Vista, Roraima (K. J. Zimmer 1). SURINAME: 8 km east of Meerzog (T. H. Davis 2, M. and P. Isler 1).

Inezia s. obscura.—BRAZIL: São Gabriel da Cachoeira, Amazonas (B. M. Whitney 3). VENEZUELA: Pto. Ayacucho, edo. Amazonas (K. J. Zimmer 2); Picua, south bank of the Río Ventuari, Yapacana National Park, Amazonas (K. J. Zimmer 3); Caño Chiguire, north bank of the Río Ventuari, Yapacana National Park, Amazonas (K. J. Zimmer 21).

Inezia s. subflava.—BOLIVIA: depto. Santa Cruz (S. L. Hilty 2). BRAZIL: Alta Floresta, Mato Grosso (B. M. Whitney 1); Amazon Lodge, Rio Juma, Amazonas (A. Whittaker 1, K. J. Zimmer 1); lower Rio Negro, Amazonas (A. Whittaker 2); Ziggylandia, west bank lower Rio Negro, Amazonas (A. Whittaker 2).

Inezia s. subflava/obscura.—BRAZIL: 35 km west of Barcelos, Amazonas (A. Whittaker 2).

APPENDIX 2

List of localities and lending institutions for specimens examined. All specimens were from one of the following institutions: American Museum of Natural History, New York (AMNH); Carnegie Museum, Pittsburgh, Pennsylvania (CM); Field Museum of Natural History, Chicago, Illinois (FMNH); Los Angeles County Museum, Los Angeles, California (LACM); Louisiana State University Museum of Natural Science, Baton Rouge, Louisiana (LSUMZ); and the Yale Peabody Museum of Natural History, New Haven, Connecticut (YPM).

Inezia s. intermedia (6 males, 2 females).—COLOMBIA: Cartagena, Bolívar (CM, 2 males); Fundación, Magdalena (CM, 1 male); Dibulla, La Guajira (CM, 1 female); Arroyo de Arenas, La Guajira (CM, 1 male). VENEZUELA: Sabana de Mendoza, Trujillo (CM, 2 males); Ocumare de la Costa, Aragua (FMNH, 1 female).

Inezia s. caudata (19 males, 11 females, 3 sex unknown).—BRAZIL: Ilha São Bento do Surrão, Roraima (FMNH, 1 female); mouth of Rio Mucajai, Roraima (LACM, 4 males, 2 females, 1 sex unknown); Flexal, Roraima (AMNH, 1 female). FRENCH GUIANA: Mana (CM, 2 males, 1 female; YPM, 3 males, 2 females). SURINAME: Leonsberg (AMNH, 1 male; LACM, 2 males; YPM, 1 sex unknown); Paramaribo (AMNH, 1 male; LACM, 1 male). VENEZUELA: Barrancas, Monagas (AMNH, 1 male); Altagracia, Bolívar (AMNH, 2 males, 1 female); Caicara, Bolívar (AMNH, 1 male, 1 female, 1 sex unknown); Ciudad Bolívar, Bolívar (AMNH, 1 male, 1 female); San Félix, Bolívar (CM, 1 female).

Inezia s. obscura (3 males, 3 females, 2 sex unknown).—BRAZIL: São Gabriel da Cachoeira, Amazonas (AMNH, 1 female); Tabocal, Amazonas (AMNH, 1 male); Camanaus, Amazonas (AMNH, 2 sex unknown). VENEZUELA: Esmeralda, Amazonas (AMNH, 2 males, 2 females).

Inezia s. subflava (17 males, 13 females, 1 sex unknown).—BOLIVIA: depto. Beni (AMNH, 1 female); Rio Paucerne, depto. Santa Cruz (LSUMZ, 1 sex unknown). BRAZIL: Borba, Amazonas (AMNH, 1 male, 1 female); Mirapinima, Amazonas (AMNH, 1 male, 2 females); Rio Tapajós, Pará (AMNH, 3 males, 3 females); Mirituba, Pará (YPM, 1 male; CM, 1 male); Rio Iriri, Pará (AMNH, 1 female); Vila Braga, Pará (CM, 1 female); Ilha das Poças, Pará (AMNH, 1 male); Bela Vista, Pará (CM, 1 male); São Raimundo, Pará (LACM, 1 male); Aveiro, Pará (CM, 1 male); Rio Xingu, Pará (AMNH, 1 male); Hupiranga, Pará (LSUMZ, 1 male); north bank Rio Amazon, site unknown (AMNH, 4 males, 4 females).

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A COMPARISON OF GARGLE CALLS OF BLACK-CAPPED CHICKADEES RECORDED IN THE LABORATORY AND IN THE FIELD

CHANDRA E. MALPEDE[1] AND MYRON C. BAKER[1,2]

ABSTRACT.—We compared recordings of the 'gargle' vocalization of Black-capped Chickadees (*Poecile atricapillus*) made in the field to recordings made in the laboratory of captive birds from the same populations. Individuals have repertoires of gargle calls, some of which are shared with conspecifics. Thus, a population sample of recordings reveals a variety of distinct gargle calls constituting the population repertoire. Captive birds were individually stimulated to vocalize by viewing their own image in a mirror. In the field, gargle calls were recorded during natural social interactions. We questioned whether the field recordings might reveal a greater variety of gargle calls than we found in the laboratory samples. We found that none of 901 field recorded gargle calls differed from those recorded from captive birds. *Received 22 June 1999, accepted 18 Oct. 1999.*

In our studies of the vocalizations of Black-capped Chickadees (*Poecile atricapillus*), we analyzed tape recordings of birds housed in sound-proof chambers in which an individual was stimulated to vocalize by viewing its image in a mirror (Censky and Ficken 1982, Baker et al. 1991). The call of interest is the gargle call, which, in nature, is given year-round primarily in close range agonistic interactions (Ficken et al. 1987) such as occur in contests over food. Each individual has a repertoire of gargle types, many of which are shared with others in the population, forming population dialects (Ficken et al. 1987; Miyasato and Baker 1999; Baker, Howard and Sweet, unpubl. data).

The question we address is whether field recordings reveal gargle call types that our laboratory assay does not. The laboratory assay has the advantage of allowing us efficiently to obtain large samples of gargle calls from marked individuals, characterize individual repertoires extensively, make detailed population comparisons, and recapture and re-record known individuals over time.

Field recording has the advantage of sampling a wide variety of social circumstances that could elicit gargle calls whose structures differ from those we found in the laboratory. Field recording of gargle calls, however, has severe limitations because, unlike recording of the advertisement songs of many territorial songbirds, chickadees for most of the year move about in small, dispersed flocks covering large home ranges, change locations often, and emit gargle calls infrequently. One can follow a flock for several hours and hear no gargle calls. Individuals may move from tree to tree when producing gargle calls, the identity of the calling bird is often not apparent (gargle calls can be emitted with no accompanying visual display), and the birds are frequently behind vegetation and hidden from the observer. Others have noted the difficulties in obtaining field samples of gargle calls of sufficient quality and quantity from marked birds (Hailman and Griswold 1996).

METHODS

Study areas.—Black-capped Chickadees were studied from October 1996 through March 1997 (hereafter the 1996–1997 season) and from October 1997 through March 1998 (hereafter the 1997–1998 season) at two sites in Fort Collins, Colorado. One site was northwest of Fort Collins at Lee Martinez Park (LMP) and the second site was southeast of Fort Collins at the Environmental Learning Center (ELC), about 8.5 km from Lee Martinez Park. Both sites are riparian habitat and connected by a continuous corridor of vegetation along the Cache La Poudre River.

Laboratory recordings.—Birds were trapped in Potter traps baited with sunflower seeds, transported to a laboratory at Colorado State University, placed in individual cages, and tape recorded in anechoic sound proof chambers (Industrial Acoustics Co.). In each chamber, small mirrors were located outside the cage and faced one end of each of the two perches. Recordings were made with a Uher 4200 Report Stereo IC recorder at tape speed 9.5 cm/s and a Uher M517 microphone placed midway between the two mirrors. After recording, the birds were banded and released at the site of capture. In this way, we made high quality

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recordings of many gargle calls in a few hours, and a number of individuals have been re-recorded several times, often over periods of several years. An analysis of these laboratory recordings will be presented elsewhere (Baker, Howard and Sweet, unpubl. data).

Field recordings.—Birds were recorded in the field in the areas covered by the trap sites at Lee Martinez Park and the Environmental Learning Center during the same two seasons of laboratory recordings. Gargle calls were recorded with a Marantz PMD 201 cassette recorder at tape speed 4.8 cm/s and a Sennheiser MD402 microphone mounted in a 60 cm parabolic reflector. At Lee Maretinez Park, 21 recording hours were distributed over 11 days in the 1996–1997 season, and 15 recording hours were distributed over 9 days in the 1997–1998 season. At the Environmental Learning Center, 7 recording hours were distributed over 5 days in the 1996–1997 season, and 27 recording hours were distributed over 22 days in the 1997–1998 season.

Analysis of recordings.—Audio tapes of recordings made in the laboratory and field were examined on a Kay Elemetrics DSP model 5500 sonagraph and printed on a Kay Elemetrics model 5510 gray-scale printer. Sonagraph settings were: frequency range DC–8 kHz (sampling rate 20,480 Hz), flat shaping, transform size 300 Hz (100 points), Hamming analysis window, and no averaging. In a typical bout of vocalizing, a bird repeats the same gargle call a number of times before switching to a different gargle call in its repertoire. For the laboratory recordings, we made sonograms of each different gargle call of each bird. Two or more birds from a recording site often shared some of their gargle calls, and some gargle calls were shared with more distant populations. Laboratory recordings of the gargle calls of different birds were independently classified into gargle groups by two observers (M.C.B. and T. M. Howard). Each gargle group, therefore, contained similar gargle calls from two or more birds.

We classified each call based on its component syllables. Syllables were examined visually on sonograms of gargle calls, each different syllable was given a unique number, and a syllable catalog was constructed from the laboratory recordings (Baker, Howard and Sweet, unpubl. data). Such syllable catalogs have been published for two other populations (Ficken et al. 1984, Hailman and Griswold 1996). Usually a syllable is formed of a single continuous trace (note) on a sonogram and is separated in time from other syllables. Sometimes a syllable is formed from a complex of notes that are never produced in isolation but always occur as a complex. Syllables are stereotyped in their frequency and time characteristics and readily recognized from one sonogram to another. Thus, each gargle call can be described as a series of numbers corresponding to the sequence of its constituent syllables. The gargle calls recorded in the field were thus compared to the gargle calls recorded in the laboratory by two independent observers (C.E.M. and M.C.B.) with an inter-observer agreement of 96%.

RESULTS

Although many of the field recordings were noisy or too faint to allow comparison of detailed acoustic features to our set of laboratory recordings, we nevertheless were able to identify most of the noisy or low amplitude gargle calls as equivalent to laboratory recorded gargle calls. We could do this because syllables are sufficiently stereotyped, and differences between types of syllables distinct enough, to identify syllables and the sequential structure of gargle calls even when they were somewhat degraded. Examples of a high quality field recorded gargle call, a low quality field recorded gargle call of the same group, and the laboratory-recorded equivalent gargle call are illustrated in Fig. 1. Those field recorded gargle calls that we could not compare with confidence because of even lower recording quality (66 out of 967 gargle calls) were not included in the analyses.

In both seasons, more gargle calls were recorded and more gargle groups identified in the laboratory recordings than were recorded and identified in the field data (Table 1). Although we know the exact number of individuals from which laboratory recordings were obtained, we do not know how many different birds contributed to the field recordings. For the field data, we assumed that we obtained a random sample of each population's gargle repertoire. Our assumption of randomness was impossible to verify, but the infrequency of gargle calls, the short bursts in which they usually occurred, and the number of days and hours spent in the populations during the recording effort led us to feel that sampling was broadly representative. A previous analysis suggests that sampling the repertoires of 5–9 birds provides a fairly complete sample of the gargle types in a population (Miyasato and Baker 1999).

The primary question we examined was whether the field recordings revealed any new kinds of gargle calls not found in the laboratory recordings. All 901 field-recorded gargle calls had equivalent gargle call types in the laboratory recordings. We also investigated the fine structure of individual syllables and made comparisons between gargle calls recorded in the laboratory and the field. To accomplish this, we ignored lower quality

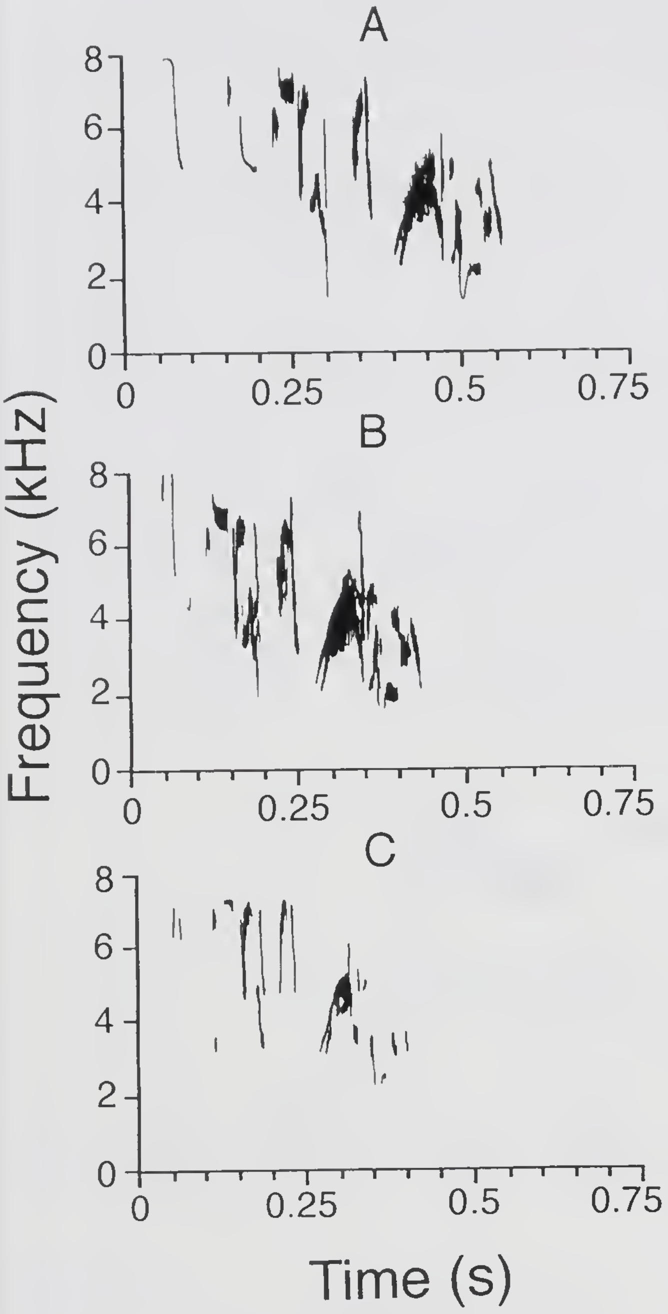

FIG. 1. Three gargle calls identified as members of the same gargle type. (A) A high-quality recording of a gargle produced in the laboratory, (B) a high-quality recording from the field, (C) a low-amplitude recording from the field.

field recordings and selected the 22 highest quality field recorded gargle calls, representing the 11 gargle groups of the Environmental Learning Center sample, and the 23 highest quality field-recorded gargle calls, representing the 10 gargle groups of the Lee Martinez Park sample, for detailed syllable-by-syllable comparison to the laboratory recordings. We each independently compared the field recorded syllables to the laboratory recorded syllables.

In these 45 comparisons, we found no gargle calls or component syllables recorded in the field that were not also recorded in the laboratory. A representative sample of three different gargle calls recorded in the field at Environmental Learning Center and their laboratory recorded matches is shown in Fig. 2. Three different gargle calls recorded in the field at Lee Martinez Park and their laboratory counterparts are shown in Fig. 3.

DISCUSSION

We conclude that Black-capped Chickadees in natural social circumstances do not display a larger variety of gargle calls than they do in the laboratory when responding to their image in a mirror. This conclusion was also reached in a previous study (Miyasato and Baker 1999) with a smaller sample of field recordings from a single location. Together these studies have examined 965 gargle calls recorded in the field in natural social circumstances and no gargle calls have been found that differ from those recorded from captive birds.

Chickadees probably draw from the same repertoire of elements in any situation eliciting gargle calling and there may be no special set of gargle calls reserved for specific contexts. It is more likely that message and meaning of gargle calling derives from the context itself (Smith 1977). Variations in the context could also be accompanied by variations in repertoire sequencing or amplitude of delivery. Even though our laboratory assay prevented vocal transactions with an opponent, and the visual stimulation unusual or infrequently encountered in nature, the repertoire expressed was made up of the same primary signal units (Smith 1991) as occur in natural social behavior. This opens the door for the investigation of how the actual performance features of gargle calling can be manipulated by varying the context of signaling in the laboratory assay.

ACKNOWLEDGMENTS

We thank T. Howard, P. Sweet, B. Francis and T. Tracy for their help with trapping, tape recording, analyses of the recordings and preparation of the illustrations. C.E.M. thanks her graduate advisory committee (B. Wright, L. Bjostad, and M. Baker) for their help. The research was undertaken by C.E.M. in partial

TABLE 1. Number of gargle calls recorded and gargle groups classified in two seasons (1996–1997, 1997–1998) in two populations (ELC: Environmental Learning Center, LMP: Lee Martinez Park) from tape recordings made in the laboratory and the field.

	1996–1997		1997–1998	
	ELC	LMP	ELC	LMP
Lab recordings				
Number of birds	10	7	9	9
Number of gargles	4985	3114	5436	8398
Number of gargle groups	24	16	12	15
Field recordings				
Number of birds	?	?	?	?
Number of gargles	109	185	225	382
Number of gargle groups	4	10	10	9

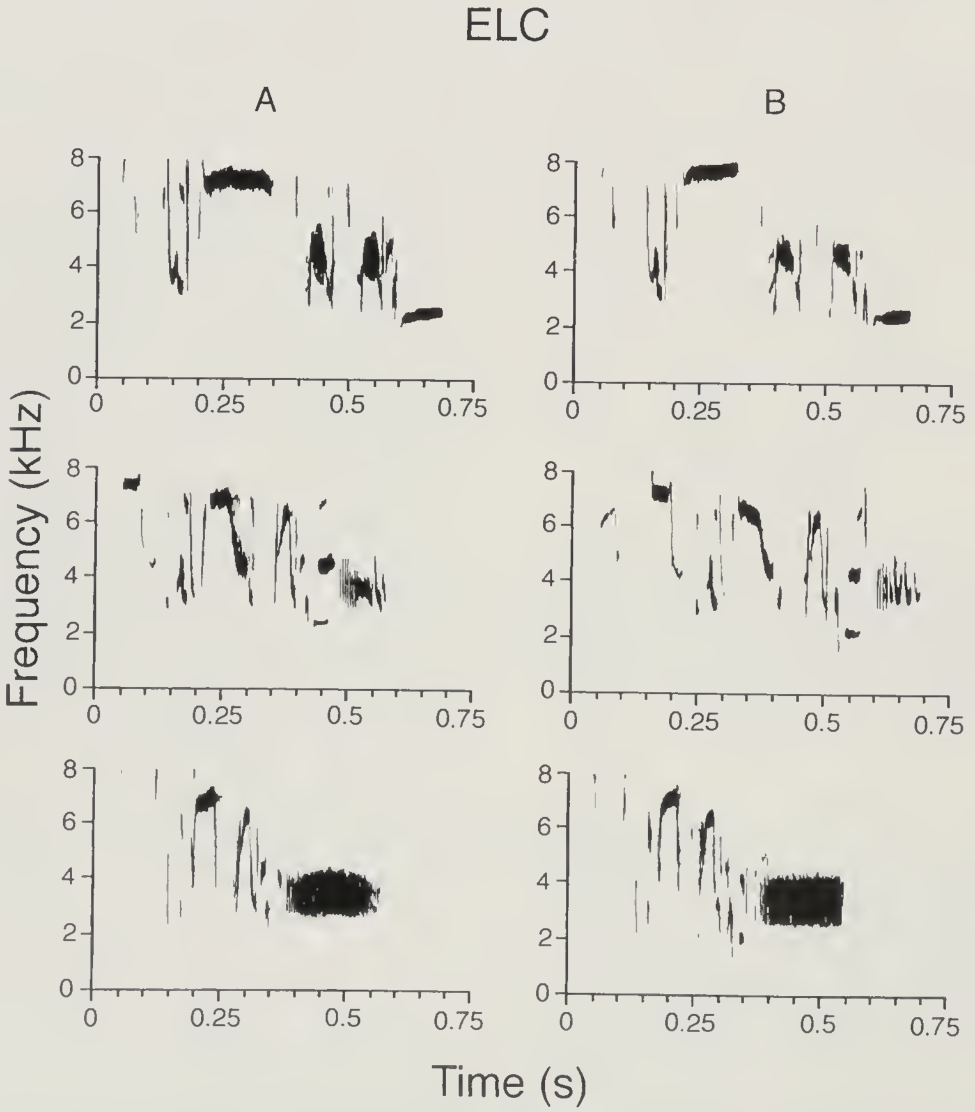

FIG. 2. Gargle calls recorded from Black-capped Chickadees from the Environmental Learning Center (ELC). (A) Calls recorded from three different birds in the field, (B) equivalent call type recorded in the laboratory.

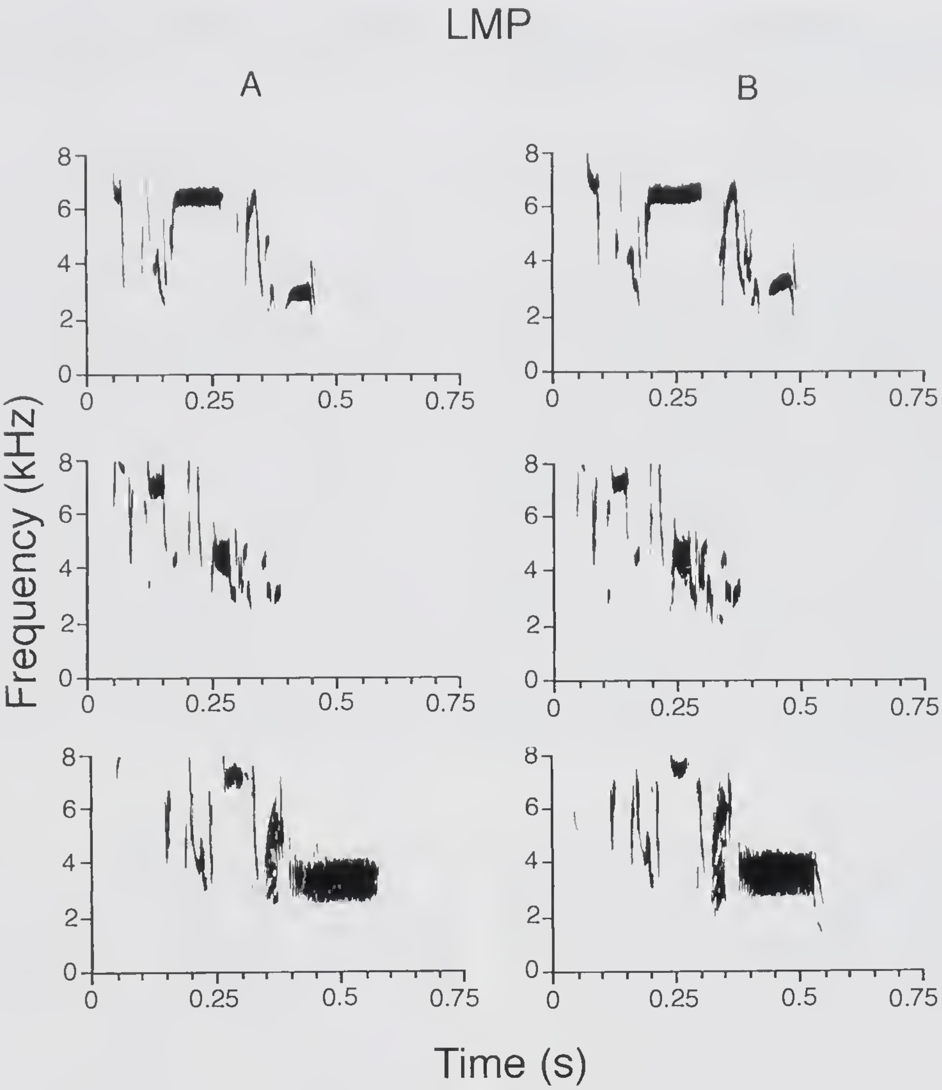

FIG. 3. Gargle calls recorded from Black-capped Chickadees from Lee Martinez Park (LMP). (A) Calls recorded from three different birds in the field, (B) equivalent call type recorded in the laboratory.

fulfillment of the requirements for the M.S. degree, Biology Department, Colorado State University.

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CONSEQUENCES OF MATE SHARING FOR FIRST-MATED FEMALES IN A POLYGYNOUS SONGBIRD, THE HOUSE WREN

STEPHEN J. CZAPKA[1] AND L. SCOTT JOHNSON[1,2]

ABSTRACT.—We investigated whether male parental assistance, reproductive output, and overwinter survival differed for female House Wrens (*Troglodytes aedon*) that did and did not have to share their mate's territories with a later-settling female during the nestling stage of breeding. During first breeding attempts of the season, when mate sharing occurred, primary females in polygynous trios and females from monogamous pairs fledged equal numbers of offspring and fledged offspring of similar mass. Rates at which males fed broods of primary females were not significantly different than rates at which males fed broods of monogamous females. Primary females did not make significantly more trips to nests to feed offspring than did monogamous females. In the first year of study, primary females were more likely than monogamous females to attempt a second brood. In the second year of the study, however, primary females tended to be less likely to attempt a second brood, took longer to start such broods, and tended to be less successful in fledging offspring from second broods. This suggests that in some years there may be a delayed cost of mate sharing. Females with primary and monogamous status for first breeding attempts in a particular year were equally likely to return to the study area the next year. Overall, our results indicate that mate sharing does not appear to affect the reproductive output of first mated females in our House Wren population in the first breeding attempts of the season, but may affect output in second attempts (and hence possibly annual and lifetime success), at least in some years. *Received 15 March 1999, accepted 20 Oct. 1999.*

Avian polygyny has been intensely studied for nearly four decades. The vast majority of studies have focused on determining why females sometimes settle with mated males, given the potential costs of mate sharing for a secondary mate (Searcy and Yasukawa 1989, Johnson et al. 1993, Slagsvold and Lifjeld 1994). Far less attention has been given to how mate sharing affects first mated or "primary" females, yet such information should be of value in understanding the evolution of avian mating systems in general (Davies 1989). For example, the widespread occurrence of monogamy in birds may result from first mated females routinely discouraging other females from settling on their mate's territory (Wittenberger and Tilson 1980, Gowaty 1995, Sandell 1998). This female-female aggression hypothesis for monogamy assumes that the presence of a secondary female on a territory is in some way costly to the primary female. Few studies have documented the nature and extent of these costs.

Potential costs of mate sharing (Bensch 1997) for primary females include: (1) competition for food, nest sites, and other resources on the male's territory; (2) reduced male assistance incubating eggs and feeding offspring because males spend time tending to the secondary female and her brood (Lifjeld and Slagsvold 1989, Pinxten et al. 1993, Sandell et al. 1996); (3) less male help watching for predators and defending nests (Hannon 1984); (4) increased exertion resulting from attempts to compensate for loss of male assistance in incubating eggs or brooding or feeding offspring (Johnson and Kermott 1993, Pinxten et al. 1993, Pinxten and Eens 1994); (5) destruction of eggs or offspring by secondary females (Veiga 1990, Bensch and Hasselquist 1994, Hasson et al. 1997), which selection should encourage because males usually shift parental attention fully to the secondary nest if the primary nest fails (Lifjeld and Slagsvold 1989, Johnson et al. 1993, Smith et al. 1994); and (6) relegation to secondary status if the primary female attempts to renest with her polygynous mate either after nest failure or for a second brood (Bensch 1996). These costs may ultimately reduce fitness of the primary female by reducing reproductive success in the current breeding attempt, future breeding attempts, or both, and by reducing the reproductive lifespan of the female.

Our objective was to assess the consequences of mate sharing for primary females

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in a polygynous population of House Wrens (*Troglodytes aedon*).

METHODS

Study species.—House Wrens are small (10–12 g), sexually monomorphic, insectivorous, cavity-nesting songbirds (Johnson 1998). Wrens return to our Wyoming study site in early May. Males sing to attract mates, and females visit territories of different males and discriminate among potential mates at least partly on characteristics of nest sites that males control (Johnson and Searcy 1993, 1996). Females usually lay clutches of 4–8 eggs with clutch size declining seasonally. Only females incubate. Males usually begin advertising for secondary mates at unoccupied nest sites on their territories when their first mates begin regular incubation (with the laying of the penultimate egg; Johnson and Kermott 1991). About 15–35% of males mate polygynously each year when most males are provided with more than 1 nest box on their territories. Clutches begin hatching 11–13 days after the last egg is laid. Both parents feed nestlings. Offspring fledge 16–18 days after hatching and are fed by one or both parents for 2 weeks thereafter.

Study site and general methods.—We conducted this study in 1996–1997 on a population of House Wrens nesting in riparian woodlands near Big Horn, Wyoming (44° 40′ N, 106° 56′ W, 1310 m). All wrens in this study were individually marked with unique combinations of colored leg-bands. We provided wrens with nest boxes mounted 1.25–1.75 m above ground on greased metal poles. Prior to wren arrival each spring, we erected two nest boxes, 25–45 m apart, on each of approximately 80 territories that had been occupied by males in previous years. Initially only one box was opened; the other was covered with a black plastic bag. We opened second boxes on the day that a male's mate laid egg 3, 4 or 5, i.e., a day or two before males normally begin advertising for secondary mates.

On many territories, the male did not attract a secondary mate by the time his first mate's eggs hatched. We were reluctant to leave extra nest sites open during first mates' nestling stages on all territories because, under natural conditions, not all males have access to a surplus nest site. A male with access to a surplus nest site during the nestling stage may modify his parental effort, putting less time into feeding offspring and more time into trying to attract an additional mate (Pinxten and Eens 1994, Smith 1995). In an earlier year when no boxes were on our site and all birds used natural cavities, about 60% of monogamous males had access to a second, natural nest cavity on their territories during their first mate's nestling stage (Johnson and Kermott 1991). We mimicked this situation by closing extra nest sites on about 40% of territories, chosen at random, starting 1–3 days before eggs began hatching on those territories.

On some territories, second boxes that we erected were claimed by "surplus" males. Such males were trapped and removed before they paired as time permitted. In a few instances, however, a surplus male had a female building a nest in his box on the day that he was removed. Subsequently, the paired male nearby quickly claimed both the box and the female, thereby obtaining a secondary mate. Such usurpatory polygyny occurs naturally in House Wrens (Freed 1986) so we included first mates of males participating in usurpatory polygyny in our sample of primary females (n = 6 of 38, 16% of primary females).

We counted numbers of offspring in nests on Nestling Days (NDs) 4, 8, 12, and 15 or 16 (where ND 1 = day on which eggs began hatching). We weighed nestlings on ND 12, the day that first-hatched offspring are at or near their maximum weight. In Illinois, nestling House Wrens that are relatively heavy on or near this day are more likely to survive to breed (C. F. Thompson, pers. comm.). In 1996, nestlings in each brood were weighed collectively to the nearest 0.1 g using a spring balance. In 1997, we switched to weighing nestlings individually to the nearest 0.01 g using an electronic balance. This allowed us to compare primary and monogamous females from 1997 not only in mean mass of nestlings produced, but also in the number of nestlings produced whose ND 12 mass was at or above the mean ND 12 mass of all nestlings fledged that year. The latter measure may provide a better indicator of how many surviving offspring a female produces in a given year, given that broods often contain nestlings that vary substantially in mass.

Parental effort.—To obtain an index of feeding effort, we documented number of feeding trips to nests by each sex during 1 h observation sessions on NDs 2, 4, 9, and 15. Number of feeding trips is equivalent to number of prey delivered because parents deliver one prey per trip (Johnson 1998). We concentrated our efforts on the early nestling stage because females brood offspring extensively at this time leaving males to provide offspring with much of their food. We observed parental feeding rates throughout the nestling stage at all primary nests each year and at as many simultaneously active monogamous nests as possible. We chose monogamous nests for observation opportunistically (e.g., many were near primary nests, minimizing our travel time). Most monogamous nests that were not observed in the early nestling stage were observed once on ND 15 or 16 to allow us to compare rates at which males deserted monogamous and primary broods before offspring fledged. Mate desertion is common in this species and is described elsewhere (Johnson 1998 and references therein). To control for diurnal variation in parental behavior, we observed nests only in the early and mid-morning hours and timed watches so that the mean start time of watches at monogamous and primary nests were similar for any given ND.

Reproductive output.—We excluded from analyses females whose nesting attempts failed during the laying or incubation stages. Almost all of these females still had monogamous status at the time of failure. To include these females in our pool of monogamous females when comparing reproductive success of primary and monogamous females would be misleading. More specifically, it allows for a greater rate of failure for monogamous females than for primary females. This is because males who acquire second mates normally do so during the late laying or incubation stage of breeding (32 of 36 cases in this study). Thus many primary females in our study became primary females only because their nests remained intact through much or all of the incubation stage. To make an accurate comparison of the consequences of mate sharing, we included in analyses only females who: (1) completed incubation and (2) began the nestling stage either with monogamous or primary status. This meant that we also excluded from analyses the four primary females who became primary females unusually late; i.e., well into their nestling stage.

In our population, only females who began their first breeding attempts relatively early in the season attempted a second brood. In comparing the frequency with which monogamous and primary females attempted second broods, we included in our analyses all monogamous and primary females who fledged at least 1 nestling from first broods and who presumably began first broods early enough in the season to attempt a second brood. This included all females who began their first breeding attempt on or before the day the last female to attempt two broods that year began her first breeding attempt (all females who laid their first egg for first broods on or before 3 June in 1996 and 2 June in 1997). Masses of nestlings produced in second attempts were not compared because we were unable to obtain nestling masses for many second nesting attempts.

Statistical analyses.—We compared frequencies using log-linear *G* tests with Williams' correction. We compared measures of parental effort using two-way ANOVA which included pairing status and year as main effects. Clutch size and other measures of reproductive output declined as the breeding season progressed. When necessary, we controlled for seasonal effects on reproductive output in two ways. First, we included in analyses only monogamous females who began laying on or before the day the last primary female of the season began laying (8 July in 1996, 5 July in 1997). Second, we compared reproductive output using analysis of covariance (ANCOVA) with date of first egg as a covariate. When ANCOVA was used, we present least-squares means; i.e., means that are directly comparable because they have been adjusted to account for differences between monogamous and primary females in time of breeding. Where possible, data for our two years were combined in a single analysis that controlled for effects of year on reproduction. In most situations, however, we encountered a significant interaction between year and pairing status (monogamous females bred more successfully in one year and primary females in the other year). This forced us to examine the effect of pairing status on reproductive output in the two years separately. We used the Statistical Analysis System (release 6.09; GLM procedure) on a VAX 6000 for analyses (SAS Institute 1985).

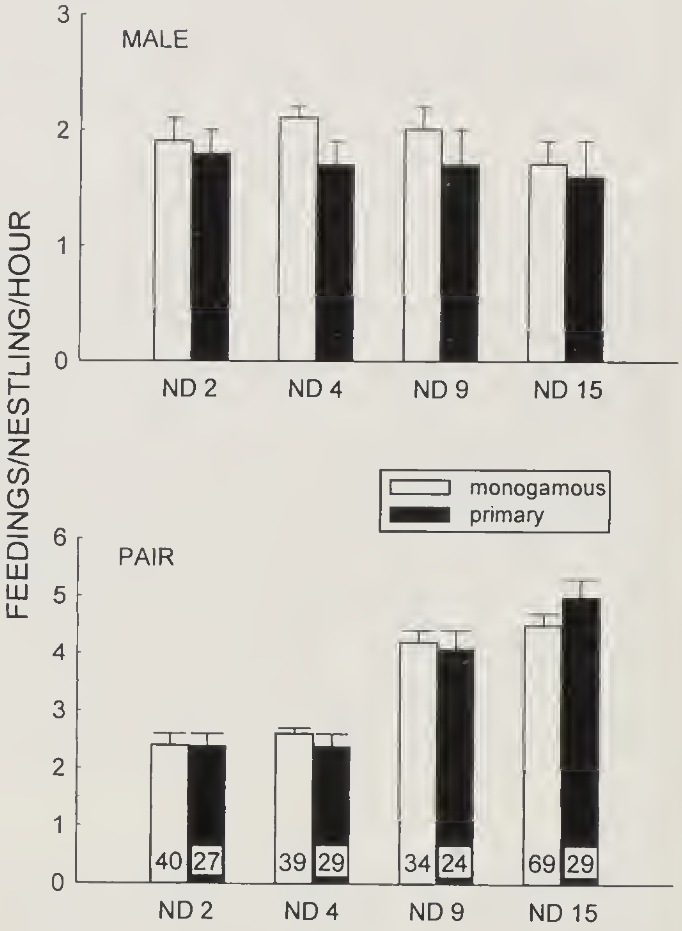

FIG. 1. Number of feedings per nestling per h at nests of monogamous and primary female House Wrens on different days of the nestling stage. Shown are means ± 1 SE with number of nests observed inside the lower bars. On Nestling Days 2, 4, and 9, none of the differences in means was significant when compared with a two-way ANOVA including year and female pairing status as main effects (all $P > 0.05$). On Nestling Day 15, non-normal distributions precluded use of ANOVA. Because feeding rates at nests of each pairing status differed very little between years, data for both years were combined and compared using a Wilcoxon rank sum test (male rates) or *t*-test (pair rates). Differences were not significant (all $P > 0.05$).

RESULTS

Parental care.—Males fed offspring in monogamous and primary nests at similar rates throughout the nestling stage (comparisons on NDs 2, 4, 9 and 15: all $P > 0.05$; Fig. 1). Polygynous males whose secondary mates were presumably fertile did not feed primary nestlings at a significantly lower rate than did males whose secondary mates were presumably infertile (comparisons on NDs 2, 4 and 9, all $P > 0.05$; Fig. 2).

The rate at which both parents combined

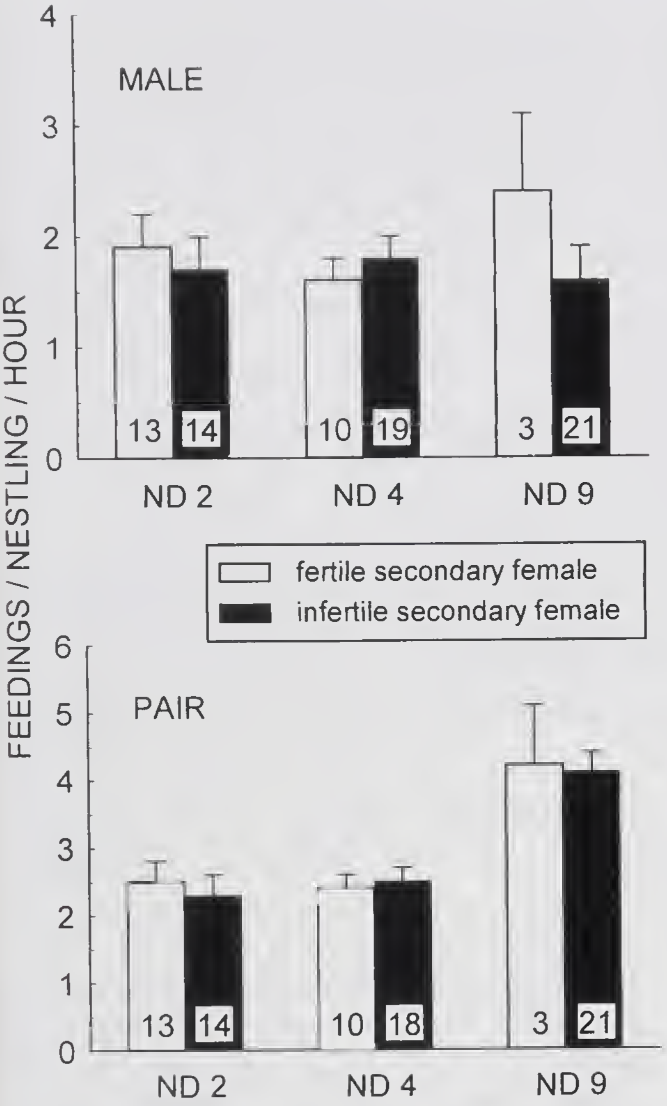

FIG. 2. Number of feedings per nestling per h at nests of primary female House Wrens when secondary females on the same territory were presumably fertile versus infertile. It was assumed that secondary females were fertile from the day that they paired through to the day that they laid their penultimate egg and began incubating. Shown are means ± 1 SE with number of nests observed inside the bars. None of the differences in means was significant when compared with a two-way ANOVA including year and secondary fertility status as main effects (all $P > 0.05$). ND = Nestling Stage Day (ND 1 = day clutch begins hatching).

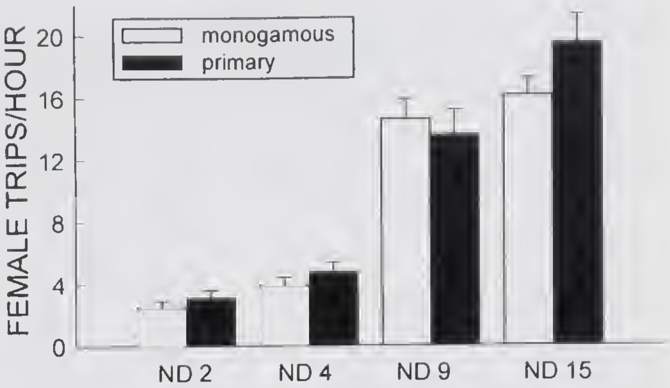

FIG. 3. Comparison of feeding effort (total trips to nest per h) by monogamous and primary female House Wrens on different days of the nestling stage. Shown are least-squares means ± 1 SE adjusted for effect of year. None of the differences in means was significant when compared with a two-way ANOVA including year and female pairing status as main effects (all $P > 0.05$). Sample sizes match those in Fig. 1.

fed nestlings did not differ significantly at primary and monogamous nests (comparisons on NDs 2, 4, 9 and 15: all $P > 0.05$; Fig. 1). We also found no significant difference in the effort that primary and monogamous females made to feed offspring as measured by total trips to nests with food, regardless of brood size (comparisons on NDs 2, 4, 9 and 15; all $P > 0.05$; Fig. 3).

Mate desertion.—Males were equally likely to desert primary and monogamous females late in the nestling stage, being absent from 11 of 29 (38%) primary nests and 28 of 70 (40%) monogamous nests on ND 15 or 16 ($G_1 = 0.04$, $P > 0.05$). Desertion seemed unrelated to the degree of synchrony in reproductive cycles of primary and secondary females: the mean interval between hatching of primary and secondary clutches was 14.1 days on territories where males deserted primary broods and 15.3 days on territories where males did not desert ($t_{27} = -0.72$, $P > 0.05$).

Polygynous males were not more likely to have deserted the primary female by ND 15 or 16 if the secondary female had hatchlings by these days as opposed to unhatched eggs. Males deserted primary broods in 5 of 14 (36%) instances where the secondary female had eggs on ND 15 or 16 of the primary brood and 6 of 15 (40%) instances where the secondary female had hatchlings at this time ($G_1 = 0.05$, $P > 0.05$).

Reproductive output in first breeding attempts.—Clutches of primary females were significantly smaller than those of monogamous females in 1996 ($F_{1,77} = 4.10$, $P < 0.05$) and larger, although not significantly so, in 1997 ($F_{1,88} = 2.42$, $P > 0.05$; Table 1). Because clutch size would not have been related to mating status (males acquire secondary mates after first mates complete clutches), we included clutch size as a covariate in comparisons of number of offspring fledged by monogamous and primary females.

Primary females tended to be more likely

TABLE 1. Reproductive output of monogamous and primary female House Wrens during first breeding attempts of the season. Shown are the means ± 1 SE with number of nests observed in parentheses.

Measure	Year	Monogamous females	Primary females	Test statistic[a]	P
Date of first egg	1996	10 Jun ± 2 d (62)	31 May ± 3 d (18)	—	—
	1997	5 Jun ± 2 d (71)	6 Jun ± 4 d (20)	—	—
Clutch size[b]	1996	6.9 ± 0.1 (62)	6.4 ± 0.2 (18)	$F_{1,77} = 4.10$	<0.05
	1997	6.8 ± 0.1 (70)	7.0 ± 0.1 (20)	$F_{1,88} = 2.42$	>0.05
Percent nests successful[c]	1996	79.4 (68)	94.4 (18)	$G_1 = 3.57$	<0.06
	1997	80.0 (75)	90.0 (20)		
No. fledglings, all nests[d]	1996	4.7 ± 0.3 (62)	5.2 ± 0.5 (18)	$F_{1,78} = 0.14$	>0.05
	1997	4.8 ± 0.3 (71)	5.0 ± 0.5 (19)	$F_{1,87} = 0.15$	>0.05
No. fledglings, successful nests[e]	1996	5.4 ± 0.2 (54)	5.6 ± 0.3 (17)	$F_{1,69} = 0.01$	>0.05
	1997	5.7 ± 0.2 (60)	5.4 ± 0.3 (18)	$F_{1,76} = 1.08$	>0.05
Mean nestling mass[f]	1996	9.8 ± 0.1 (36)	10.0 ± 0.2 (16)	$F_{1,127} = 1.96$	>0.05
	1997	9.8 ± 0.1 (61)	10.0 ± 0.2 (18)		
No. fledglings ≥ mean mass[g]	1997	3.6 ± 0.2 (62)	3.5 ± 0.4 (16)	$F_{1,75} = 0.03$	>0.05

[a] Where possible and appropriate, data for two years were combined in a single analysis that controlled for effects of year on reproduction. When a significant interaction occurred between year and pairing status, tests were made for each year separately.

[b] Shown are least-squares means adjusted for effect of breeding date; F-test from ANCOVA with first egg date as covariate.

[c] Successful nests produced ≥1 fledgling. G from log-linear test.

[d] Shown are least-squares means controlling for effect of clutch size from a parametric ANCOVA; F-test from Quade's Rank ANCOVA (Huitema 1980) with clutch size as a covariate.

[e] Shown are least-squares means adjusted for effect of clutch size and year from a parametric ANCOVA; F-test from Quade's Rank ANCOVA with clutch size as a covariate.

[f] Shown are least-squares means controlling for effects of year and breeding date; F-tests for effect of pairing status in ANCOVA with first egg date as covariate.

[g] Mean mass = mean mass of fledglings in 1997 (9.90 g). Data available for 1997 only. Shown are least-squares means adjusted for effect of clutch size; F-test for effect of pairing status from ANCOVA with clutch size as covariate.

than monogamous females to fledge at least 1 nestling (92% vs 80% of attempts, respectively; $G_1 = 3.57$, $P < 0.06$; Table 1). Main causes of nest failure were complete brood starvation (3% and 9% of primary and monogamous broods, respectively) and destruction of offspring following takeover of the territory by a conspecific male (affecting 0% and 7% of primary and monogamous attempts, respectively).

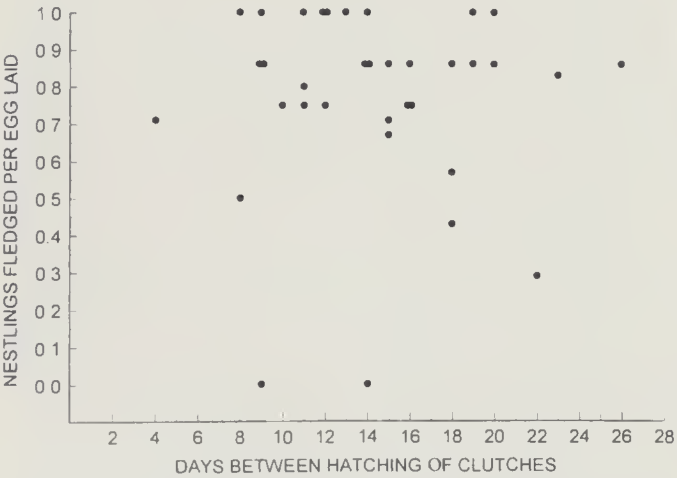

FIG. 4. Relationship between number of days elapsing between hatching of clutches of the primary and secondary female on territories of polygynous male House Wrens and fledging success (number of offspring fledged per egg laid) of the primary female (Spearman rank correlation: $r_s = -0.02$, $n = 35$, $P > 0.05$).

There was no significant difference in the number of offspring fledged by monogamous and primary females in either year (1996: $F_{1,78} = 0.14$, $P > 0.05$; 1997: $F_{1,87} = 0.15$, $P > 0.05$; Table 1). Monogamous and primary females did not differ significantly in the proportion of eggs that they hatched successfully [0.91 ± 0.03 ($n = 34$) vs 0.92 ± 0.01 ($n = 101$); $t_{133} = 0.59$, $P > 0.05$], or in the proportion of hatched offspring that they fledged [0.91 ± 0.03 ($n = 34$) vs 0.89 ± 0.02 ($n = 101$); $t_{133} = 0.59$, $P > 0.05$]. Mean mass of offspring in primary broods was not significantly different from that of offspring in monogamous broods in either year ($F_{1,127} = 1.96$, $P > 0.05$).

Considering all nests, successful and unsuccessful, fledging success at primary nests was unrelated to the degree of nesting synchrony between primary and secondary nests ($r_s = -0.02$, $n = 35$, $P > 0.05$; Fig. 4). However, the mean mass of offspring in primary broods declined significantly as the interval between the hatching of primary and secondary clutch-

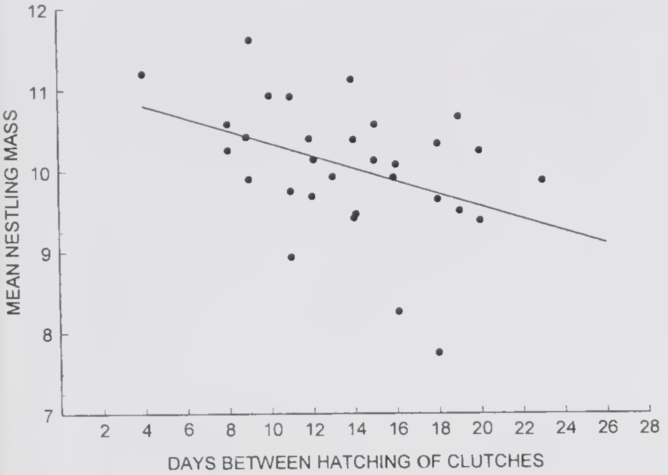

FIG. 5. Relationship between number of days elapsing between hatching of clutches of the primary and secondary female on territories of polygynous male House Wrens and the mean mass of offspring produced by primary females on Nestling Stage Day 12 (Spearman rank correlation: $r_s = -0.40$, $n = 30$, $P < 0.03$). Nestling Stage Day 1 = day clutch begins hatching.

es increased ($r_s = -0.40$, $n = 30$, $P < 0.03$; Fig. 5).

Reproductive output in second breeding attempts.—A significantly greater proportion of primary than monogamous females attempted second broods in 1996 (56% vs 21% of females, respectively; $G_1 = 5.21$, $P < 0.03$) but not in 1997 (43% vs 63% of females, respectively; $G_1 = 1.56$, $P > 0.05$; Table 2). In 1996, the mean time elapsing between first and second attempts of females classified as primary or monogamous in first attempts did not differ (35.7 vs 35.8 d, respectively; $t_{13} = 0.02$, $P > 0.05$). In 1997, however, primary females took significantly longer to initiate second clutches than did monogamous females (43.0 vs 37.6 d; $t_{28} = -2.42$; $P < 0.02$; Table 2).

There was no significant difference between primary and monogamous females in size of clutches laid for second breeding attempts in either year (1996: $F_{1,12} = 1.94$; $P > 0.05$; 1997: $F_{1,28} < 0.01$, $P > 0.05$; Table 2). Nor did we find a significant difference either year in the proportion of second attempts that were successful ($P > 0.05$ for both years), although sample sizes for primary females were quite small in each year (Table 2). In 1996, primary and monogamous females did not differ substantially in mean number of offspring fledged from second nests ($Z = 0.06$, $P > 0.05$; Table 2). In 1997, however, on average, primary females fledged two (60%) fewer offspring from second nests than did monogamous females ($Z = -1.91$, $P < 0.06$; Table 2).

Annual reproductive output.—Females with monogamous and primary status in first breeding attempts did not produce significantly different numbers of fledglings over the course of the entire breeding season in 1996 or 1997 (both $P > 0.05$; Table 3).

Return rates of females.—The probability of a female returning to our site was unrelated

TABLE 2. Comparison of reproductive output in second breeding attempts of the season for female House Wrens that had either monogamous or primary mating status in first attempts. Shown are means ± 1 SE with number of nests observed in parentheses.

Measure	Year	Monogamous females	Primary females	Test statistic	*P*
Frequency of second attempts[a]	1996	6/28 (21.4%)	9/16 (56.3%)	$G_1 = 5.21$	<0.03
	1997	25/40 (62.5%)	6/14 (42.9%)	$G_1 = 1.56$	>0.05
Interclutch interval[b]	1996	35.8 ± 1.7 (6)	35.7 ± 1.8 (9)	$t_{13} = 0.02$	>0.05
	1997	37.6 ± 0.9 (24)	43.0 ± 2.5 (6)	$t_{28} = -2.42$	<0.02
Clutch size[c]	1996	5.3 ± 0.3 (6)	4.9 ± 0.3 (9)	$F_{1,12} = 1.94$	>0.05
	1997	5.5 ± 0.2 (25)	5.5 ± 0.3 (6)	$F_{1,28} < 0.01$	>0.05
Number of nests successful[d]	1996	4/6 (66.7%)	9/9 (100.0%)	FET[e]	>0.05
	1997	19/25 (76.0%)	3/6 (50.0%)	FET[e]	>0.05
No. of fledglings, all nests	1996	3.2 ± 1.0 (6)	3.6 ± 0.5 (9)	$Z = 0.06$[f]	>0.05
	1997	3.5 ± 0.5 (24)	1.5 ± 0.7 (6)	$Z = -1.91$[f]	<0.06

[a] Shown is number of females attempting second broods/total number of females that presumably fledged offspring from first broods early enough to attempt a second brood (see text). *G* from log-linear test.

[b] Equals total days elapsing between the last egg of the first brood and the first egg of the second brood.

[c] Shown are least-squares means adjusted for breeding date. *F*-test for effect of status from ANCOVA with first egg date of second brood as covariate.

[d] "Successful" nests produced ≥1 fledgling.

[e] FET = two-tailed Fisher's exact test.

[f] *Z* scores from Wilcoxon Rank Sum tests.

TABLE 3. Total number of offspring fledged over the course of the entire breeding season for monogamous and primary female House Wrens. Included in analyses are all females that presumably completed first breeding attempts early enough to make a second attempt (see text for specific criteria). Not all females made second attempts. Number of nests observed are in parentheses. Shown are least-squares means ± 1 SE from ANCOVA with first egg date of first brood as covariate.

Year	Monogamous females	Primary females	Test statistic	*P*
1996	6.8 ± 0.4 (31)	6.9 ± 0.6 (17)	$F_{1,45} = 0.04$	>0.05
1997	7.5 ± 0.5 (45)	6.0 ± 0.8 (15)	$F_{1,57} = 1.70$	>0.05

to the number of broods she had reared the previous year: females returned in 40 of 137 (29%) versus 18 of 48 (38%) instances where they had reared one and two broods the previous season, respectively ($G_1 = 1.10$, $P > 0.05$). Including single and double brooded females in a single analysis, we saw females the next season in 43 of 146 (29%) instances where females had monogamous status the previous season versus 15 of 39 (38%) instances where females had primary status ($G_1 = 1.11$, $P > 0.05$).

DISCUSSION

We found no evidence to suggest that mate sharing reduces the reproductive output of primary females in polygynous trios of House Wrens, at least during first breeding attempts of the season when mate sharing occurs. In each of two years, primary females fledged as many offspring as did monogamous females, and offspring fledged by primary and monogamous females were of similar weights suggesting similar prospects of surviving to breed. In fact, primary females tended to be more likely than monogamous females to fledge at least one nestling because primary females lost fewer broods to starvation or destruction by conspecifics.

Primary females in our study were probably not, as a group, older and more experienced than monogamous females and hence more capable breeders. In the second year of study (1997) 50% of primary females and 48% of monogamous females had at least one year's breeding experience. Although we could not make the same comparison for 1996 (because few females were marked in 1995), we note that primary females laid significantly smaller clutches than did monogamous females in 1996 which suggests that, if anything, primary females were less capable breeders than monogamous females this year.

Primary females may have reproduced equally as well as monogamous females during first breeding attempts of the season for reasons other than age or experience. First, mate sharing simply may not be immediately costly for primary females; i.e., all else being equal, females would usually breed equally well with or without a secondary female present. Consistent with this, rates at which males fed primary broods were, on average, not significantly lower than rates at which males fed monogamous broods.

Alternatively, there may normally be some immediate proximate costs to mate sharing for primary females but such females are compensated for these costs by having access to better-than-average territorial resources (nest sites, food, cover, etc.) or perhaps genetic resources (resulting in the production of more viable offspring; e.g., Kempenaers et al. 1992). This would allow primary females to breed as successfully as monogamous females who have, on average, lower quality breeding situations. In Chiffchaffs (*Phylloscopus collybita*), primary females appear to produce about 30% more offspring than monogamous females in part because primary females more frequently occupy higher quality habitat than do monogamous females (Rodrigues 1996). In our study, for example, access to high quality food resources might have allowed primary females to compensate for any reduction in rates at which their mates feed offspring (see also Bensch 1996).

We cannot determine whether breeding situations of primary females in our study were, on average, of higher quality than those of monogamous females. One might expect this to be the case if primary females settled earlier in the season than monogamous females giving primary females a better selection of territories and mates. Primary females settled earlier than the monogamous females to whom they were compared in 1996, and bred more successfully than monogamous females in this one year. To distinguish between the "no-cost" and "compensation-for-costs" explanations for the equal success of primary and monogamous females, one would have to remove secondary females from a randomly selected group of territories and compare the success of primary females on those territories to that of unmanipulated primary females. The no-cost hypothesis predicts equal success for experimental and control females while the compensation-for-costs model predicts that experimental females would outperform control females.

Although mate sharing did not seem to affect female reproductive output during the concurrent breeding attempt, our study does suggest that mate sharing may affect female success at producing second broods in some years. In 1996, primary females were more likely to make a second breeding attempt and tended to be more successful in second attempts than monogamous females. In contrast, in 1997, primary females tended to make fewer second breeding attempts and fledged fewer offspring from those attempts when compared to monogamous females. Numbers of second breeding attempts observed each year were small, especially for primary females, and our data must therefore be viewed with some caution. Further comparisons of annual fitness in females that do and do not share mates certainly seem warranted, however.

In some polygynous species, males provide more feeding assistance to secondary females when primary and secondary nesting cycles overlap extensively and the age difference between primary and secondary broods is small. Reproductive output of primary females declines as overlap in primary and secondary nesting cycles increases in some species, for example, in Pied Flycatchers (*Ficedula hypoleuca*; Lifjeld and Slagsvold 1989, 1990) and Blue Tits (*Parus caeruleus*; Kempenaers 1995) but not others, for example, European Starlings (*Sturnus vulgaris*; Sandell et al. 1996). In our study, we found no relationship between the extent of overlap in nesting cycles of primary and secondary females and the number of offspring fledged per egg laid for primary females. However, the mean weight of offspring produced by primary females was lowest when primary and secondary cycles overlapped relatively little. One potential explanation for this result is that if secondary females settle late, just before or just after primary eggs hatch, the fertile period of the secondary female will overlap the first part of the primary female's nestling stage when offspring require brooding and male aid is most essential (Johnson et al. 1992, Johnson and Kermott 1993). Polygynous Red-winged Blackbird (*Agelaius phoeniceus*) males are less likely to feed offspring of an early settling mate when a later settling mate is in her fertile period (as opposed to her pre- or postfertile period; Whittingham 1994). In our study, however, feeding rates of males to primary broods seemed unaffected by the fertility status of the secondary female. Why a primary female tends to produce lighter nestlings when settlement of the secondary female comes late in her nesting cycle remains unclear.

We used nest boxes mounted on greased poles which eliminated nest predation. We chose to eliminate nest predation entirely because rates and patterns of predation on nests in boxes do not match those for nests in natural cavities, even if boxes are mounted on trees (Johnson and Kermott 1994). Under natural conditions, approximately 30% of nesting attempts on our site fail, many probably as a result of predation. Note that elimination of nest predation makes our results more conservative since more secondary females completed nesting attempts than would be expected under natural conditions; that is, we increased the extent to which some primary females had to share mates and hence increased our chances of documenting a cost of mate sharing for primary females. Elimination of nest predation might be a concern if, under natural conditions, primary females normally suffered higher rates of predation than monogamous females. However, we have no reason to suspect that nests of primary females are depredated more than nests of monogamous females.

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OBSERVATIONS OF WOOD THRUSH NEST PREDATORS IN A LARGE CONTIGUOUS FOREST

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ABSTRACT.—We used inexpensive (<$30) cameras to document predators at active Wood Thrush (*Hylocichla mustelina*) nests in Great Smoky Mountains National Park. We observed such predators as black rat snakes (*Elaphe obsoleta*), American Crows (*Corvus brachyrhynchos*), southern flying squirrels (*Glaucomys volans*), and black bears (*Ursus americanus*) remove the contents of nests. Camera installation had no measurable effect on nest survival; daily nest survival was approximately 0.96 for nests with and without cameras. However, placement of an artificial egg trigger in the nest appeared to reduce hatching success. The immobile egg trigger might have interfered with the female Wood Thrush's ability to incubate her eggs. The variety of nest predators observed and the moderate daily survival rates recorded suggest that predation is an important constraint on Wood Thrushes nesting in large contiguous forests. *Received 18 March 1999, accepted 25 August 1999.*

The primary cause of nest failure among forest nesting passerines is predation (Ricklefs 1969, Martin 1993). The prevailing fragmentation hypothesis suggests that predation rates are higher in fragmented landscapes than in contiguous forest (Robinson et al. 1995). This pattern has been demonstrated for several species of Neotropical migrants, including Wood Thrushes (*Hylocichla mustelina*) whose populations have experienced consistent declines in recent years (Robbins et al. 1989, Peterjohn et al. 1995). Studies in small to moderate sized forest fragments consistently have shown an inverse relationship between forest patch size and nest predation rates (Wilcove 1985, Donovan et al. 1995, Hoover et al. 1995, Robinson et al. 1995, Weinberg and Roth 1998). In contrast, data from 416 nests monitored over five breeding seasons in Great Smoky Mountains National Park suggest that the inverse relationship between forest patch size and nest predation rates may disappear or even reverse when habitat patches exceed size or disturbance thresholds (Farnsworth 1998, Farnsworth and Simons 1999). Average daily nest survival rates in the park (the largest contiguous tract of forest in the eastern U.S.) were substantially less than those reported in studies on moderately large forest tracts (Farnsworth and Simons 1999). These findings suggest that while daily nest survival rates may increase with forest patch size at intermediate spatial scales, they may level off or even decline in very large and protected patches, resulting in what Suarez and coworkers (1993) have called the "paradox of predation."

Although it is generally agreed that predation is an important influence on forest songbird populations, it is surprising how little direct evidence is available about nest predators. Many authors have listed potential songbird nest predators, including American Crows (*Corvus brachyrhynchos*), Blue Jays (*Cyanocitta cristata*), raccoons (*Procyon lotor*), squirrels, and snakes (see Martin 1988, Yahner and DeLong 1992, Roth et al. 1996). Other authors have attempted to attribute nest failures to predators based on eggshell remains in the nest and nest disturbance (e.g., Johnson 1979, Moors 1983). However, when Marini and Melo (1998) presented captive predators (reptiles, birds, and mammals) with eggs, they found that eggshell remains were not diagnostic of the predator involved. This result casts doubt on studies that use nest remains to categorize predators. Interestingly, none of the 86 snakes (comprising 22 species) tested by Marini and Melo consumed eggs in captivity. Roper and Goldstein (1997) obtained a similar result. They tested 12 genera of snakes and found only one genus, *Pseustes*, that ate eggs in captivity.

Some researchers have used cameras at artificial nests to document potential predators (e.g., Laurance and Grant 1994, Picman and Schriml 1994, Danielson et al. 1996). However predators of artificial nests may not be the same as those of active nests (Major and Kendal 1996). Few studies have been able to

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identify the predators at natural nests. Some have been able to document predators at active nests using expensive time-lapse video or movie cameras (e.g., Henson and Grant 1992, Booth et al. 1996, Brown et al. 1998, Thompson et al. 1999). While these systems can be effective, their cost generally limits their application to a small number of nests. A notable exception is the study by Major and Growing (1994), which identified predators at New Holland Honeyeater (*Phylidonyris novaehollandiae*) nests. They used inexpensive automated cameras to photograph nests at the moment the contents were being eaten. They identified the primary predator as black rats (*Rattus rattus*).

In this paper, we present results obtained from an inexpensive camera system developed to identify the predators at Wood Thrush nests in Great Smoky Mountains National Park. Understanding the relative importance of the predators responsible for nest failures in this relatively pristine habitat may shed light on the relatively low daily nest survival rates recorded in the park and may provide a baseline for comparisons to studies on more fragmented landscapes.

STUDY AREA AND METHODS

Great Smoky Mountains National Park straddles the border of North Carolina and Tennessee, encompassing an elevation range from 300–2020 m. Since its establishment as a National Park in 1934, all logging has been prohibited and forest fires have been controlled, creating one of the largest contiguous tracts of forest (202,000 ha) in the eastern U.S. We located and monitored Wood Thrush nests in the park from 1995 to 1997 as part of a larger study (Farnsworth 1998, Farnsworth and Simons 1999). Once located, nests were visited once every three days. We placed cameras to document nest predators during three breeding seasons. Not all nests we found were suitable for camera installation. Therefore the sample of nests at which we installed cameras was not random. We were restricted to installing cameras at nests low enough to allow us access with a 1.8 m (6 ft) ladder.

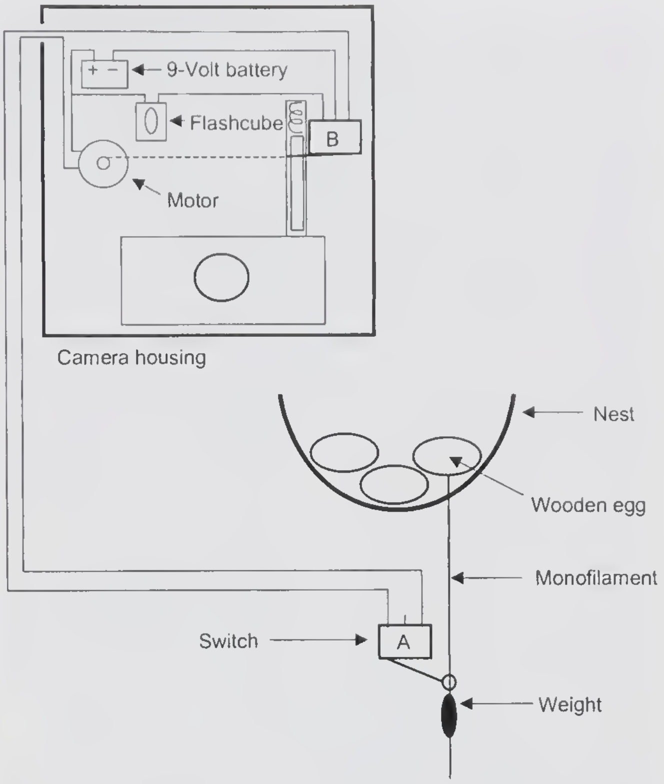

FIG. 1. Schematic of nest monitoring camera and egg trigger. When the wooden egg was lifted, switch A closed the circuit from the battery to the motor. The motor pulled a string (dotted line) attached to a pin (not pictured). Removal of the pin released a spring-loaded dowel and activated switch B. Switch B closed the circuit from the battery to the flashcube and opened the circuit from the battery to the motor. The dowel then depressed the shutter release on the camera taking a picture.

Camera units consisted of an inexpensive fixed focus camera ($5.00; model AK41ZL promotional 35 mm camera from Two Jays Inc., Mount Holly, New Jersey) housed within a plastic food container painted green (Fig. 1). The camera was triggered by an egg placed in the nest (alongside the natural eggs in active nests or as a single egg in a recently depredated nest) and tethered to a relay by a short section of monofilament (40 lb. test). We used a Northern Bobwhite (*Colinus virginianus*) egg with a mechanical relay in 1995, and a painted wooden egg with an electronic relay in 1996 and 1997. The electronic relay was far more reliable and consisted of a submini lever switch (Catalog part # 275-016A; Radio Shack) mounted on the trunk or a horizontal branch below the nest. The monofilament was threaded through an eye-hook glued to the lever switch. A fishing weight was attached to the monofilament below the eye-hook. The switch was connected to the camera housing via 22 guage electrical wires (approximately 7 m in length). The camera housing contained a 9 volt battery forming two circuits, one to the motor (Catalog part # 273-223; Radio Shack) and one to the flashcube. When the trigger egg was lifted, switch A (Fig. 1) closed the circuit with the motor. The motor pulled a pin that was holding a spring-loaded dowel. The dowel was held in a PVC pipe with a notch cut into it. The pin prevented the dowel from depressing the shutter-release button on the camera. Removal of the pin also activated a second submini lever switch. Activating this switch simultaneously turned off the motor and sent current to the flashcube. It was necessary to activate the flashcube before depressing the shutter-release button because approximately 10 milliseconds were required to illuminate the flashcube. Once a flash picture was taken, there was no further drain on the battery because all circuits were open. Therefore the total battery usage with this system was minimal (< 1 sec per photograph), and a camera unit could remain operational for several weeks. We mounted cameras at least 1 m from nests (usually on a nearby tree), and in most cases could complete an installation in 5 min. The cost of all materials was approximately $30.00 per unit.

To examine the effect of the disturbance caused by installing cameras, we compared the daily survival rate (Mayfield 1975) of nests with cameras to the daily survival rate of nests without cameras using a z-test (Johnson 1979). We compared the hatching rate of eggs in nests with and without cameras installed. It usually takes 2 days for all the eggs in a clutch to hatch (Roth et al. 1996). Therefore, only nests observed initially with eggs and later with chicks at least 3 days old were included in this analysis. Eggs found in nests with chicks 3 days old or older were considered to have failed to hatch. We used a G-test of independence to test if the hatching rate of eggs was independent of the presence of a trigger egg in the nest. Because the hatching of each egg within a clutch is not independent, we compared the proportion of camera and non-camera nests in which at least one egg failed to hatch using a G-test of independence. All statistical tests were performed with SAS (version 7) under Windows NT 4.0.

RESULTS

We installed camera units at 57 active Wood Thrush nests. Eleven of these nests were apparently abandoned immediately, and two other nests were initially accepted but abandoned a few days after installation. The camera unit was triggered by the attending Wood Thrush on three occasions. Seventeen nests eventually fledged young. Nineteen cameras were installed on nests after a predator had already visited an active nest (four nests belonged to both groups). The camera unit failed to take a picture when the contents of the nest were disturbed or removed on 18 occasions. A photograph was recovered but no predator was visible on 11 occasions.

We documented eight different species of predators removing eggs from active or recently depredated Wood Thrush nests. Of 19 photographs taken of predators, 7 were records of predation at active nests, and 12 were records of predators at recently depredated nests. At active nests we obtained two pictures each of American Crows (*Corvus brachyrhynchos*), black rat snakes (*Elaphe obsoleta*), and black bears (*Ursus americanus*) and one picture of an Eastern Screech-Owl (*Otus asio*). Three of these photographs (one each of American Crow, black bear, and Screech-owl) were taken at nests with Wood Thrush chicks, the remainder at nests with eggs. In addition to the photographs, we have good evidence of bear predation from two other nests. In these cases nest trees were found clawed and bent over, and the nests were destroyed.

The 12 pictures from recently depredated nests included 5 crows, 3 southern flying squirrels (*Glaucomys volans*), a black rat snake, least weasel (*Mustela rixosa*), white-footed mouse (*Peromyscus leucopus*), and gray squirrel (*Sciurus carolinensis*). Three of the crow pictures were obtained from the same nest (after first recording a flying squirrel) and the other was from one of the active nests described above.

We compared the nesting success of nests with camera units installed to nests without camera units. There were 3167.5 exposure days and 136 failures at nests without cameras (285 nests) and 604 nest exposure days and 25 failures where cameras were installed and accepted (46 nests). The resulting daily survival rate estimates, 0.957 [± 0.004 (SE)] for nests without cameras and 0.959 (± 0.008) for nests with cameras, were not different ($z = 0.17$, $P > 0.05$).

Cameras were accepted by incubating adults at 45 nests and 24 (53%) of these nests survived to hatching as defined above. The average number of days of incubation between camera installation and hatching was 9.7 days. Hatching success at nests without cameras was 0.949 (332 of 350 eggs hatched). At nests with cameras, eggs hatched at a rate of only 0.869 (73 chicks hatched from 84 eggs). The reduction in hatching probability was significant (G-test of independence: $G_{adj} = 5.67$, 1 df; $P = 0.017$). Fifteen of 100 control nests had at least one unhatched egg, and 10 of 24 nests with cameras failed to hatch at least one egg ($G_{adj} = 7.24$, 1 df; $P < 0.01$).

The amount of time between camera installation and hatching did not appear to affect the probability of hatching. We divided nests with cameras into two groups, those at which incubation continued for fewer than 10 days before hatching and those incubated for more than 10 days. Hatching rates in the two groups were nearly identical (0.870 vs 0.868 respectively; $G_{adj} < 0.01$, 1 df; $P > 0.05$).

DISCUSSION

We are encouraged that a simple inexpensive camera system can provide new insights into the causes of forest songbird nest predation. An artificial egg trigger added to an active nest appears to be effective for documenting a variety of nest predators during both the incubation and the nestling stages. The daily survival rates of nests with cameras were no different from nests without cameras suggesting that the effect of the cameras on the nesting birds is minimal.

We made substantial improvements to the cameras during the study; however, more improvement is possible. In 1996 a number of cameras failed when the switch below the nest (switch A; Fig. 1) got wet and shorted the battery. Waterproofing the switch resolved the problem. Because we did not want to alter the visibility of nests by removing vegetation, it was difficult in many situations to mount the camera with a clear line of sight to the nest. As a result 11 pictures were taken at depredated nests but no evidence of a predator could be found on the photograph.

Addition of a tethered egg to the clutch may have caused nest abandonment and reduced hatching success in some nests. The tethered egg triggers were fixed to a piece of stiff monofilament that kept the egg from moving in the nest. On one occasion, we installed a camera at a nest on 3 June 1997 and on 6 June, the nest was discovered to be abandoned and the wooden egg had been damaged, suggesting the Wood Thrush returned to the nest and attempted to remove the wooden egg. The trigger egg may also have inhibited the female's ability to turn the other eggs in the clutch and may have reduced hatching success. Periodic rotation of eggs during incubation is necessary to ensure proper development of the embryo (Drent 1975). A more flexible egg trigger (perhaps incorporating a proximity switch instead of a tether) may more closely mimic a real egg, making it more likely to be accepted and less likely to reduce hatching success.

We were not able to place cameras at all nests discovered. Many nests were too close to heavily used hiking trails, other nests were too high for us to reach, even with a ladder. Therefore our results may represent an incomplete or biased sample of Wood Thrush nest predators on our study sites. The camera system described here could probably be successfully adapted for use on ground or low shrub nesting species such as Ovenbirds (*Seiurus aurocapillus*) and Hooded Warblers (*Wilsonia citrina*). We successfully installed cameras at nests of both of these species during our study.

Another potential bias associated with using automated cameras is that cameras may attract predators. Although we found no increase in predation rates at nests with cameras compared to nests without cameras, we do not know if the predators at these two types of nests were similar. Predators may also learn to associate cameras with a reward of eggs. Among the photographs taken at active nests, no two pictures of the same predator species were taken within 30 km of each other, suggesting that we did not observe an individual predator learning to associate cameras with eggs. We did record the same species (presumably the same individual) up to three times at the same nest.

In light of recent studies with captive snakes (Roper and Goldstein 1997, Marini and Melo 1998), it is noteworthy that we photographed a black rat snake removing a quail egg from a nest that had failed a few days earlier. The egg was at ambient temperature, suggesting that the snake may have been returning to a nest it had discovered previously. Similar observations were made of crows and flying squirrels returning to recently depredated nests. Installing cameras at nests after they fail may be an effective and less intrusive technique for documenting nest predators.

This work is a small step toward developing better techniques for understanding the effects of predation on Wood Thrush and other forest songbirds. We found a diversity of predators responsible for the relatively high rate of Wood Thrush nest failures in Great Smoky Mountains National Park. The park, a large and relatively undisturbed protected area within a largely forested Southern Appalachians landscape, represents a relatively pristine habitat where the effects of forest fragmentation on natural communities should be minimal.

Similar studies conducted in other large forests as well as small and medium-sized forest fragments, are necessary to understand how nest predation varies with landscape composition and land use.

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FLOCKING AND FORAGING BEHAVIOR OF WINTERING PROTHONOTARY WARBLERS

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ABSTRACT.—We quantified flocking behavior and examined the impact of social context (solitary, single-species flocks, and mixed-species flocks) on the foraging behavior of Prothonotary Warblers (*Protonotaria citrea*) wintering in a Costa Rican mangrove forest and surrounding habitats. Based on observations collected over two winters during 70 visits to four sites, 87% (483) of the 555 Prothonotary Warblers encountered moved in flocks and over 48% (271) of these individuals were in single-species flocks. Although the propensity to join flocks was 6% higher for Prothonotary Warblers in the second winter of the study, neither the average size of single-species flocks nor the average number of individuals or species in mixed-species flocks differed between years. Twenty-seven different species were identified in mixed-species flocks that had at least one Prothonotary Warbler, but Nearctic migrants dominated these flocks. Analyses of focal observations on 57 females and 93 males indicated that Prothonotary Warbler foraging behavior was largely independent of flock type and size. Foraging maneuver, substrate, and location did not differ significantly for individuals of either sex foraging alone, in single-species, or mixed-species flocks. The species is almost strictly insectivorous, gleaning made up 70% of 150 prey capture attempts observed and about half of all attempts (76 of 150) were directed towards leaf surfaces. Foraging generally occurred in the outer third of the tree, on branches less than 1 cm in diameter, in the bottom half of the canopy. Agonistic interactions among flock members that involved Prothonotary Warblers were uncommon and neither flock type nor size were useful predictors for rates of foraging, movement, preening, or vigilance. *Received 14 May 1999, accepted 14 Oct. 1999.*

Various costs and benefits have been hypothesized for individuals that associate with foraging flocks (see reviews by Moynihan 1962, Morse 1977, Powell 1985). Compared to solitary foragers, members of such groups gain increased protection from predation through greater overall vigilance and predator detection by the group (Pulliam 1973, Kenward 1978) and lessened individual probability of predation (Hamilton 1971, Lazarus 1979). Similarly, group members may benefit from enhanced foraging opportunities as a result of a decreased requirement for individual vigilance (Powell 1974, Popp 1988) and through copying the foraging behavior of more successful individuals in the group (Krebs et al. 1972, Morse 1978, Waite and Grubb 1988). However, it also has been suggested that the benefits of predator protection within flocks may come at the cost of decreased feeding efficiency (Rabenold and Christensen 1979, Hutto 1988). Competition among flock members for resources, as well as the potential need to adjust foraging behavior to match the movement patterns of other members in the flock, could hinder foraging effectiveness (Austin and Smith 1972, Alatalo 1981, Petit and Bildstein 1987).

In addition to flock size, species composition may influence foraging behavior and thus alter the relative costs and benefits of membership in a group. Mixed-species flocks may have less inter-individual competition for food than similarly sized flocks of conspecifics (Fretwell 1972, Barnard and Thompson 1985, Hogstad 1988). Some species substantially alter their foraging behavior when in flocks of differing compositions (Valburg 1992, Latta and Wunderle 1996). However, there have been relatively few studies to compare the foraging behavior of individuals in a population where they may forage as single individuals, in single-species flocks, and in mixed-species flocks. We present data describing the foraging behavior of Prothonotary Warblers (*Protonotaria citrea*) wintering in Costa Rica. Our goals were to describe the composition of foraging flocks which include Prothonotary Warblers, assess differences in the propensity of Prothonotary Warblers to form flocks across

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years, and compare the foraging behavior of individual Prothonotary Warblers in flocks of different composition. We examined these data to determine if there were any differences within the sexes and between males and females in their foraging tactics, locations, and rates of foraging behavior while associated with flocks of different composition and size.

STUDY SITE AND METHODS

We conducted field work from November through January during the boreal winters of 1990–1991 and 1991–1992 at Tivives, Puntarenas, Costa Rica (9° 52′ N, 84° 42′ W; Fig. 1). We used narrow foot trails along the edge of coastal mangrove forest and in the adjacent hillside woods to survey study sites. Inland edges of the mangrove were dominated by black mangroves (*Avicennia germinans* and *A. bicolor*) with canopy heights ranging from 3–10 m; pure stands of red mangrove trees (*Rhizophora racemosa*), covering about 60% of the entire mangrove, occupied the central portion with canopy heights ranging from 25–30 m (see Jiménez 1988 for details). Soil in the black mangrove sections of the forest remained damp throughout the two study periods; only during the monthly inundation associated with spring tides was there standing water in these areas. Adjacent hillsides were covered in sec-

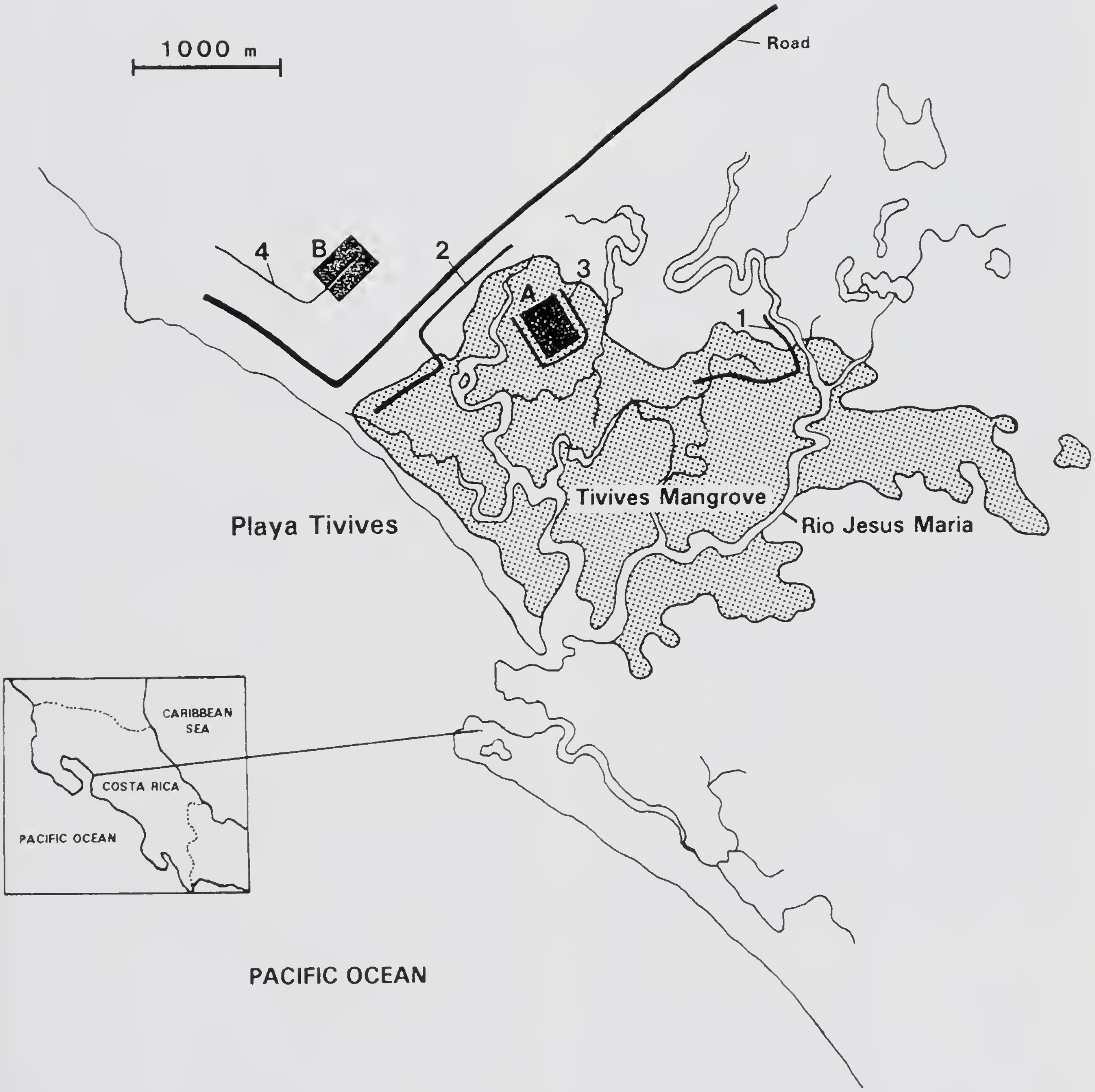

FIG. 1. Map of Tivives mangrove and surroundings showing the two trapping areas (A = Mangrove Trap Area, B = Hillside Trap Area) and four trails used for behavioral observations (1 = Turnaround Road, 2 = Access Road Mangrove, 3 = Trap Area, and 4 = Hillside Trail).

ond-growth forest dominated by guacimo (*Guazuma ulmifolia*), cecropia (*Cecropia peltata*), and poro-poro (*Cochlospermum vitifolium*), creating a canopy 7–10 m high, with emergent Guanacaste trees (*Enterolobium cyclocarpum*) up to 30 m tall.

Four transects (indicated on Fig. 1) were established to make foraging observations of Prothonotary Warblers: (1) Turnaround Road, 250 m along a 5-m wide strip of gallery forest on the river bank flanked by rice fields and cattle pastures, then 750 m running along the northern edge of the mangrove in a 10–50 m wide band of *Avicennia*; (2) Access Road Mangrove, 500 m in a 3–15 m wide band of *Avicennia* on the western edge of the mangrove, then 1000 m of roadway parallel to the western edge of the mangrove at the base of the adjacent hillside; (3) Trap Area, a perimeter trail along mist-net lanes in the 4.8 ha area of *Avicennia* in the northwestern corner of the mangrove with a total length of just over 1000 m; (4) Hillside Trail, 600 m in second-growth forest along net lanes, then 400 m up a ravine with a small permanent creek (1 m wide) which runs perpendicular to the mangrove.

We surveyed the four transects nine times each year with the exception of the Access Road Mangrove and Turnaround Road transects which had eight visits in winter 1991–1992. To reduce the possibility of encountering and recording data for the same individual or flock, each transect was surveyed no more frequently than once every seven days from November through January each year. One transect was completed each day between 05:30 and 10:30 local time by walking slowly along the trails listening for call notes and watching for activity. Progress along the trail was interrupted to observe individual Prothonotary Warblers and flocks of two or more birds that included at least one Prothonotary Warbler. For the purposes of this paper, we followed Powell (1985) who defined flocks as cohesive units that form through contact with other individuals in the group and move together. We considered all individuals within 10 m of one another, which appeared to be joining or following one another (regardless of species), to be members of the flock. Prothonotary Warblers were classed as members of a single-species flock if all potential flockmates were of the same species. Prothonotary Warblers in any flock that included, on the basis of the criteria listed above, individuals of at least one other species were considered to be a members of a mixed-species flock.

For each Prothonotary Warbler encountered we recorded age and/or sex, bands and color bands, the number, age and/or sex of associated conspecifics within 10 m of each other, the species and number of other associated birds within 10 m, time, and location. The maximum distance that we followed any individual or flock was approximately 50 m, so the chance that a species "joined" a flock simply by having that flock move into its territory was reduced. We compared the flocking propensity (Hutto 1994) of Prothonotary Warblers between years, as well as the relative proportions of migrants and residents in mixed-species flocks, using χ^2 analyses (all analyses were conducted using SAS version 6.03 on a Unix platform; SAS Institute Inc. 1988). The number of Prothonotary Warblers in single-species flocks and the number of Prothonotary Warblers and individuals of other species in mixed-species flocks, as well as the number of species in those flocks, were compared between years based on Mann-Whitney *U*-tests where parametric test assumptions were violated. A *t*-test was used to compare the mean number of Prothonotary Warblers in single-species flocks versus mixed-species flocks with data from both years pooled.

Once social context was ascertained, focal observations were made of individual Prothonotary Warblers to characterize and compare general foraging behavior for males and females in each flock type (solitary, single-species flock, and mixed-species flock). This analysis was based on the collection of data for one foraging maneuver for a single male and female in each flock. Circumstances did not always allow for each of these data points to be collected for all flocks encountered because of flock composition or movements. In related research, 164 Prothonotary Warblers were captured at two locations on the study site (see Fig. 1) and individually marked with a combination of colored, plastic leg bands and U.S. Fish and Wildlife Service numbered aluminum leg bands (see Warkentin and Hernández 1995 for details). Although fewer than 8% (42) of the 555 Prothonotary Warblers we encountered during these transects were color banded, we made every effort not to record behavior for the same individual more than once per transect to reduce the potential for producing autocorrelated data (Wagner 1981). To avoid bias for more conspicuous foraging behaviors, such as sallies that might draw attention to a particular individual or type of maneuver, we based our assessment on the first foraging maneuver seen 10 s after beginning observations on the individual. For each focal individual we recorded the following information based on the location of the bird, rather than its potential prey, because only a small percentage of foraging attempts were aerial: (1) height of the foraging bird estimated to the nearest 1 m; (2) canopy height estimated to the nearest 1 m below 10 m and to the nearest 2.5 m above 10 m; (3) perch diameter estimated to be ≤ 0.5, 1, 2, or 3+ cm; (4) horizontal position in the canopy of the perch tree relative to the trunk was categorized as inner ⅓, middle ⅓, or outer ⅓; (5) foraging substrate was classified as leaf, bark, ground, dead leaf, or air; (6) prey type where visible; and (7) foraging maneuver. We classified foraging maneuvers into three major categories based on the descriptions of Remsen and Robinson (1990). Accuracy of categorization was high as these observations were made from distances of less than 5 m using close-focusing binoculars. All behavioral data were collected by the senior author. Gleans were those near-perch maneuvers where the bird picked prey items from a substrate surface without leaving the perch. Gleaning included reaches, hangs, and lunges as well as foraging from surfaces when no acrobatic movements were required. Probes also were classified as near perch ma-

TABLE 1. Flocking behavior of Prothonotary Warblers during two boreal winters in forested habitats of Tivives, Costa Rica. Values presented include the number of encounters with each type of social grouping plus, where appropriate, the mean number ± SE and range (all in parentheses) of Prothonotary Warblers seen in single-species and mixed-species flocks, and the mean number of individuals of other species in mixed-species flocks.

	1990–1991	1991–1992
Solitary Prothonotary Warblers	45	27
Single-species flocks	32	28
	(4.5 ± 0.5, 2–13)	(4.5 ± 0.6, 2–13)
Mixed-species flocks	24	30
Prothonotary Warblers	(3.7 ± 0.6, 1–11)	(4.1 ± 1.0, 1–32)
Other species	(4.1 ± 0.7, 1–14)	(4.4 ± 0.6, 1–13)

neuvers but entailed an insertion of the bill into a substrate to extract hidden prey items. Sallies were wing-powered aerial maneuvers where the bird flew from a perch to attack the prey and then returned to a perch. Differences in foraging behavior (i.e., foraging maneuver, substrate, perch diameter, and position in the tree) for male and female Prothonotary Warblers in each flock type and between the sexes were compared using χ^2 analyses. Where necessary, cells were collapsed to ensure adequate sample size (following the criteria described by Zar 1996). We examined data on foraging height and foraging height as a function of canopy height using a general linear model (PROC GLM, SAS Institute Inc. 1988). Because of the strong correlation between height of perch and canopy height ($r^2 = 0.68$, $n = 150$, $P < 0.001$), only the analysis of perch height is included.

We also were interested in how rates of behavior might change with the composition or size of the flock. To assess variation in behavior between individuals in groups of different composition (solitary individuals, single-species, or mixed-species flocks) and size (1, 2–5, 6–9, and 10+ individuals), sequential observations were collected from members of the same flocks discussed above and transformed into rates of behavior (observations per 100 s). Observations of a single focal individual were continued as long as possible to a maximum of 10 minutes, although the average length of contact was 96 s. In addition to the data on position and foraging maneuver listed above, we recorded the pace of movement by focal individuals through the habitat (hops and flights of all lengths), preening activity (cleaning feathers, bill wiping, and scratching), social interactions (intra- and interspecific), and vigilance (scanning the environment for potential predators or competitors, which was indicated by positioning the head such that the bird obviously was not looking at near-perch surfaces for prey). Recorded observations were timed during transcription to determine the rates of occurrence for each of these behaviors. We used a general linear model (PROC GLM, SAS Institute Inc. 1988) to analyze log-transformed data (of the variable value itself plus the minimum non-zero value for that variable) for foraging rates (all maneuver types combined), preening, scanning, and movement between perches. This treatment of the data provided a better distribution pattern than the typical transformations recommended for proportions (e.g., arcsine; Zar 1996).

RESULTS

Flocking behavior.—During the 36 transects completed in the 1990–1991 season, we encountered 279 Prothonotary Warblers; 34 transect visits in the 1991–1992 season resulted in the sighting of 276 Prothonotary Warblers. These encounters included sighting solitary individuals, as well as birds in single-species flocks, and mixed-species flocks (Table 1). The propensity for Prothonotary Warblers to join flocks varied between years with 83.9% (234) of 279 individuals seen participating in flocks during the 1990–1991 season and 90.2% (249) of 276 individuals seen in flocks during the 1991–1992 season ($\chi^2 = 4.396$, df = 1, $P < 0.05$). However, there were no significant differences between years in the median number of Prothonotary Warblers found in single-species flocks and mixed-species flocks, or the median number of individuals of other species in mixed-species flocks (Mann-Whitney *U*-tests: respectively, $U = 462.5$, $U = 389$, $U = 384$; $P > 0.05$ in all cases; see Table 1 for sample sizes). Nor was there a significant difference between the mean number of Prothonotary Warblers in single-species flocks (mean ± SE reported throughout: 4.5 ± 0.4, $n = 60$) and mixed-species flocks (3.9 ± 0.6, $n = 54$) when both years were combined (*t*-test: $t = 0.813$, df = 112, $P > 0.05$). There were no significant differences between years in the number of species involved in mixed-species flocks (1990–1991: 3.9 ± 0.4 species, 1991–1992: 3.2 ± 0.2 species; $U = 442.0$, $P > 0.05$).

The list of species observed with Prothonotary Warblers in the 54 mixed-species flocks seen over both years contains 11 migrants and 15 residents (Table 2) with an average of 3.5 species per mixed-species flock (range: 2–8 species). Tennessee Warblers (*Vermivora peregrina*) were the most common other member of mixed-species flocks containing Prothonotary Warblers and made up 40% (92) of 230 individuals in 31 of these mixed-species flocks. Overall in mixed-species flocks containing at least one Prothonotary Warbler, migrants outnumbered residents by about 5 to 3 (144 versus 86).

Foraging behavior.—Based on observations of 57 females and 93 males made during the transects in both years, foraging maneuver was independent of flock type for both females ($\chi^2 = 1.57$, df = 4, $P > 0.05$; Fig. 2a) and males ($\chi^2 = 2.82$, df = 4, $P > 0.05$; Fig. 2b). The proportional use of foraging maneuvers, pooled across flocking types, was not significantly different between females and males ($\chi^2 = 2.57$, df = 2, $P > 0.05$). Likewise, foraging substrate was independent of flock type for females ($\chi^2 = 6.99$, df = 4, $P > 0.05$; collapsed to leaf, bark and others because of sample size; Fig. 3a) and males ($\chi^2 = 4.33$, df = 6, $P > 0.05$; based on leaf, dead leaf, bark, and others; Fig. 3b), with no significant difference between females and males in substrate use pooled across flock types ($\chi^2 = 6.23$, df = 3, $P > 0.05$; based on leaf, dead leaf, bark, and other) in their use of foraging substrates. In general, gleaning made up 70% (105) of 150 prey capture attempts by females and males, with about half of all attempts (76 of 150) directed towards leaf surfaces. Of the 150 foraging events observed, only 2 were directed towards non-arthropod targets, one involved eating berries and the second taking nectar.

Data on the location of these foraging individuals within the canopy or tree also suggest no differences on the basis of social structure or sex. Perch diameter was independent of flock type among females ($\chi^2 = 0.48$, df = 4, $P > 0.05$; collapsed to ≤ 0.5, 1 and 2+ cm because of sample size; Fig. 4a) and males ($\chi^2 = 9.64$, df = 6, $P > 0.05$; Fig. 4b), with no association between sex and perch diameter pooled across flock types ($\chi^2 = 3.65$, df = 3, $P > 0.05$). Similar results were obtained when we examined the association between position in the canopy and flock type (females: $\chi^2 = 4.51$, df = 4, $P > 0.05$, Fig. 5a; males: $\chi^2 = 6.87$, df = 4, $P > 0.05$, Fig. 5b; sex vs perch position: $\chi^2 = 1.85$, df = 2, $P > 0.05$). Likewise, perch height was not influenced by either sex or flock type (GLM: $F_{5,144} = 0.35$, $P > 0.05$). In general, most observed perches were in the outer third of the tree (116 of 150), primarily on branches smaller than 1 cm diameter (89 of 150), frequently in the bottom half of the canopy (mean of perch height/canopy height = 0.33), and averaged 3.0 ± 0.2 m above ground (range: ground to 10 m with 66% of observations 3 m or lower).

With the exception of female scanning behavior, for which flock type was a useful predictor of scan rate (GLM: $F_{1,71} = 4.86$, $P < 0.05$), flock type and flock size had no influence on rates of behavior (scanning, foraging maneuver, movement, and preening events per minute) during foraging, as we measured it (Tables 3, 4). There were no significant interaction effects between flock type and size for any of the variables examined. Agonistic interactions (supplanting from perches or chasing) between members of flocks were not common. Of the 7 occasions when such interactions were observed, 5 involved Prothonotary Warblers in mixed-species flocks (2 intraspecific interactions and 3 interspecific interactions) and the other 2 were in single-species flocks (extended chases by adult males of an adult male in one case and an adult female in the other). These rates of occurrence were not significantly different ($\chi^2 = 0.85$, df = 1, $P > 0.05$).

DISCUSSION

Knowledge of Prothonotary Warbler ecology on its nonbreeding grounds is limited. Although several studies have provided information of a largely qualitative nature on foraging (e.g., Post 1978, Hespenheide 1980, Morton 1980), detailed quantitative data on flocking and foraging behavior for wintering Prothonotary Warblers are only available from one study in Venezuela (Lefebvre et al. 1992, 1994). In addition, this species is of interest as one of a group of migrant (both Nearctic and Neotropical) and resident birds dependent upon mangrove habitats in Latin America

TABLE 2. The number of mixed-species flocks containing Prothonotary Warblers observed in forested habitats of Tivives, Costa Rica, and the number of occasions on which each of the other species listed below was recorded in those flocks.

		Co-occurring species																									
Species	*n*	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
1 *Protonotaria citrea*	54	31	13	12	11	7	6	6	5	5	4	3	3	3	3	3	2	2	2	2	1	1	1	1	1	1	1
2 *Vermivora peregrina*	31		7	6	5	5	4	2	3	2	4	1	1	1	3	2	2	1	2	2	1	1	0	0	1	1	0
3 *Dendroica petechia erithachorides*	13			0	0	3	2	4	1	3	0	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1	0
4 *Polioptila albilorus*	12				0	0	0	0	2	0	4	1	1	1	1	0	0	0	0	0	1	0	1	0	0	0	0
5 *Setophaga ruticilla*	11					1	3	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
6 *Lepidocolaptes souleyetii*	7						1	1	0	1	0	0	0	0	1	1	0	1	1	1	0	0	0	0	0	1	0
7 *Mniotilta varia*	6							1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
8 *Seiurus noveboracensis*	6								0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
9 *Dendroica petechia*	5									1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
10 *Todirostrum cinereum*	5										0	0	0	0	2	2	0	0	1	2	0	0	0	0	0	0	0
11 *Icterus galbula*	4											0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0
12 *Vireo flavifrons*	3												0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
13 *Tityra inquisitor*	3													0	1	0	0	0	0	0	1	0	0	0	0	0	0
14 *Thryothorus pleurostictus*	3														0	0	0	0	0	0	0	0	0	0	0	0	0
15 *Pachyramphus agleiae*	3															1	0	0	2	2	1	0	0	0	0	0	0
16 *Vermivora pinus*	3																0	0	1	2	0	0	0	0	0	0	0
17 *Piranga rubra*	2																	0	0	0	0	0	0	0	0	0	0
18 *Helmitheros vermivorus*	2																		0	0	0	0	0	0	0	0	0
19 *Hylophilus decurtatus*	2																			2	0	0	0	0	0	0	0
20 *Sittasomus griseicapillus*	2																				0	0	0	0	0	0	0
21 *Euphonia luteicapilla*	1																					0	0	0	0	0	0
22 *Arremonops rufivirgatus*	1																						0	0	0	0	0
23 *Tolmomyias sulphurescens*	1																							1	0	0	0
24 *Trogon melanocephalus*	1																								0	0	0
25 *Seiurus auricapillus*	1																									0	0
26 *Dendrocolaptes certhia*	1																										0
27 *Troglodytes aedon*	1																										

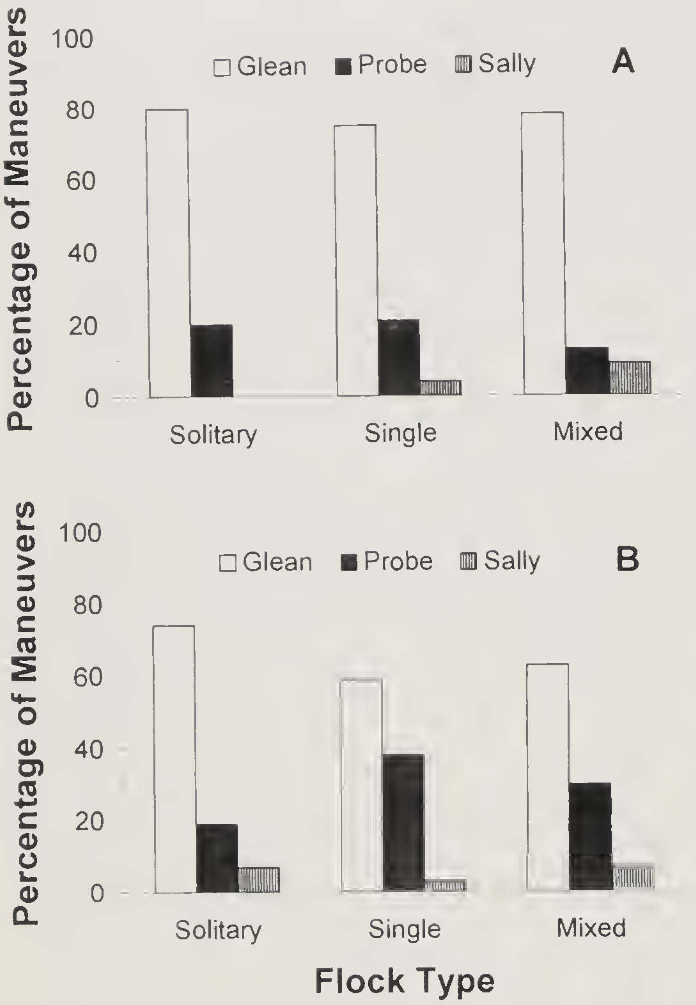

FIG. 2. Foraging maneuvers by flock type for (A) females [Solitary $n = 10$, single-species flocks (Single) $n = 24$, mixed-species flocks (Mixed) $n = 23$] and (B) males (Solitary $n = 31$, Single $n = 32$, Mixed $n = 30$).

FIG. 3. Foraging substrate use by flock type for (A) females [Solitary $n = 10$, single-species flocks (Single) $n = 24$, mixed-species flocks (Mixed) $n = 23$] and (B) males (Solitary $n = 31$, Single $n = 32$, Mixed $n = 30$). Other category includes soil surfaces, aerial sallys, nectar sources and fruit.

(ffrench 1966, Hutto 1980, Russell 1980, Lynch 1989, Styles and Skutch 1989, Lefebvre et al. 1992, Warkentin and Hernández 1995). Such species face an uncertain future as mangrove forests continue to be degraded or lost through timber harvest, coastal development and pollution, and the expanding aquaculture industry (Leonard 1987, Terborgh 1989, Olson et al. 1996).

A large proportion of the Prothonotary Warblers we encountered during this study moved in flocks and almost half of the birds seen over both years were in single-species flocks (Table 1). The tendency for this species to form single-species flocks during winter has been noted previously on a qualitative basis for Panama (Hespenheide 1980, Morton 1980). However, Post (1978) never observed single-species Prothonotary Warbler flocks in a limited sample from Puerto Rico, nor did Lefebvre and coworkers (1994) during their more extensive work in Venezuelan mangroves. In both cases, Prothonotary Warblers were seen foraging only in mixed-species flocks or alone (Post 1978, Lefebvre et al. 1994). The propensity for Prothonotary Warblers in this study to join flocks increased from winter 1990–1991 to winter 1991–1992. But each of the three social groupings was well represented in both years, and within flock types (mixed-species flock and single-species flock) there were no significant differences between years in the sizes of the flocks or the average number of member species in mixed-species groups.

Hutto (1994) suggested that insectivorous mixed-species flocks in western Mexico are often chance associations whose membership can be predicted on the basis of species abundance in the area. Across the Neotropics, mi-

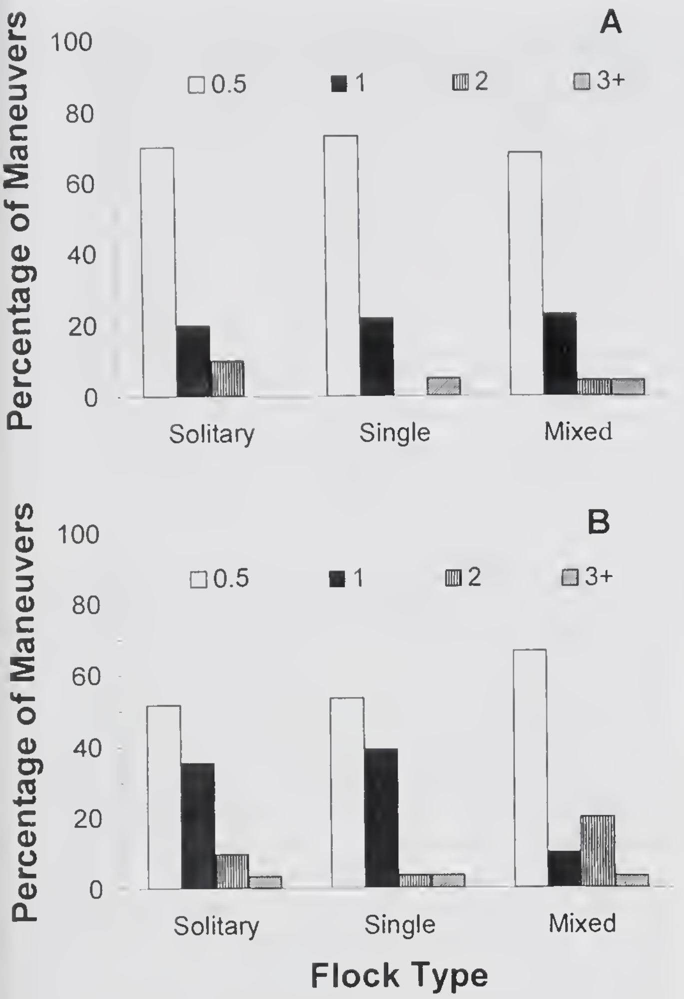

FIG. 4. Foraging perch diameter by flock type for (A) females [Solitary *n* = 10, single-species flocks (Single) *n* = 22, mixed-species flocks (Mixed) *n* = 22] and (B) males (Solitary *n* = 31, Single *n* = 28, Mixed *n* = 30). Diameter categories are in cm.

FIG. 5. Foraging location within the canopy by flock type for (A) females [Solitary *n* = 10, single-species flocks (Single) *n* = 22, mixed-species flocks (Mixed) *n* = 21] and (B) males (Solitary *n* = 31, Single *n* = 27, Mixed *n* = 30). Canopy positions were inner ⅓, middle ⅓, and outer ⅓.

grants often take part in these mixed-species flocks but typically constitute only a minor component (Powell 1985). An exception to this is within mangrove forest where migrants are more numerous than residents when compared with the surrounding habitats (Hutto 1980, Lynch 1989), and numerically dominate mixed-species flocks (this study). Among mixed-species flocks at Tivives containing at least one Prothonotary Warbler, the most consistent flockmate for Prothonotary Warblers was the Tennessee Warbler (Table 2). The dominance of migrants, such as Prothonotary and Tennessee warblers, in these flocks may simply reflect the high percentage of Nearctic

TABLE 3. Rates (mean ± SE per 100 s) of scanning, foraging, moves between perches, and preening by Prothonotary Warblers in single-species flocks (Single), mixed-species flock (Mixed), or foraging alone (Alone) in forested habitats of Tivives, Costa Rica during two boreal winters.

Sex	Flock	*n*	Scan	Forage	Move	Preen
Male	Alone	32	1.8 ± 0.4	7.1 ± 1.1	15.3 ± 1.7	2.2 ± 1.0
	Single	40	1.5 ± 0.4	6.1 ± 0.8	14.9 ± 1.3	1.3 ± 0.5
	Mixed	35	1.4 ± 0.5	5.9 ± 0.9	14.3 ± 0.9	2.0 ± 0.7
Female	Alone	8	2.7 ± 1.2	8.0 ± 1.7	13.6 ± 2.3	2.0 ± 2.0
	Single	43	1.4 ± 0.4	4.8 ± 0.7	16.0 ± 0.9	2.0 ± 0.7
	Mixed	25	0.4 ± 0.3	8.9 ± 2.0	16.0 ± 1.7	0.5 ± 0.2

TABLE 4. Rates (mean ± SE per 100 s) of scanning, foraging, moves between perches, and preening by Prothonotary Warblers for flocks of varying sizes in forested habitats of Tivivies, Costa Rica during two boreal winters.

Sex	Flock size	*n*	Scan	Forage	Move	Preen
Male	1	32	1.8 ± 0.4	7.1 ± 1.1	15.3 ± 1.7	2.2 ± 1.0
	2–5	52	1.2 ± 0.3	5.5 ± 0.6	15.4 ± 1.0	1.6 ± 0.5
	6–9	16	1.8 ± 0.6	7.5 ± 1.6	13.6 ± 1.2	1.3 ± 0.7
	10+	7	2.3 ± 2.0	6.8 ± 2.0	11.2 ± 2.5	2.4 ± 1.8
Female	1	8	2.7 ± 1.2	8.0 ± 1.7	13.6 ± 2.3	2.0 ± 2.0
	2–5	35	0.8 ± 0.2	6.3 ± 1.0	16.2 ± 1.2	0.5 ± 0.2
	6–9	20	1.4 ± 0.7	4.7 ± 1.7	15.2 ± 1.3	2.8 ± 1.1
	10+	13	1.1 ± 0.6	9.1 ± 2.5	16.8 ± 2.3	1.9 ± 1.1

migrants that occupy this mangrove forest during the boreal winter (Warkentin and Hernández 1995). Prothonotary Warblers constituted 30% (216) of the 708 migrants captured at Tivives during mist-netting over two winters (Warkentin and Hernández 1995), and the only other species caught in large numbers were Mangrove Warblers (*Dendroica petechia erithachorides*) and Northern Waterthrush (*Seiurus noveboracensis*); both of which are territorial and unlikely to join a foraging flock (Schwartz 1964, Wiedenfeld 1992). Thus chance associations may explain not only the high percentage of migrants in the mixed-species flocks of mangroves, but also the large proportion of single-species Prothonotary Warbler flocks we encountered at this site. Overall, there were few other migrants or residents for Prothonotary Warblers to join with that foraged in a similar niche.

Joining a mixed-species flock has been suggested to have costs in terms of a reduced foraging niche (Powell 1985), changes in foraging behavior (Valburg 1992, Latta and Wunderle 1996), or convergence among members on the foraging behavior of the nuclear species (Morse 1970, Valburg 1992; but only Buskirk 1972, cited from Powell 1985, recorded convergence of foraging maneuvers by insectivores). Given our limited sample size for some of these comparisons, we may not have been able to detect subtle changes in behavior between individuals foraging alone, in single-species flocks, or in mixed-species flocks. But neither were there any substantive changes evident in our comparisons of maneuver type (Fig. 2), foraging substrate (Fig. 3), perch diameter (Fig. 4) and position (Fig. 5), or rates of movement and preening (Tables 3, 4) that could be related to flock composition or size. Even vigilance and foraging rates, two elements hypothesized to change in response to foraging context (Morse 1977, Powell 1985), were largely unaffected by flock composition or size, with the notable exception that females were less vigilant in mixed-species flocks.

Increased intra- and interspecific competition and reduced risk of predation are two factors that individuals must balance in assessing the relative costs and benefits of flock membership. We found that the average number of Prothonotary Warblers in single-species flocks and mixed-species flocks was not significantly different (respectively, 4.5 and 3.9; Table 1). In terms of competition, this suggests that intraspecific competition among Prothonotary Warblers would remain consistent for individuals pursuing either flocking strategy, but those who join mixed-species flocks face the added interspecific competition of mixed-species flocks from an average 4.2 other individuals (Table 1). In contrast to reports that indicate that aggressive interactions are a common feature of mixed-species flock foraging (Morse 1970, Munn and Terborgh 1979, Powell 1985), we rarely observed such encounters. A limited sample of seven observations, based on 54 mixed-species flocks with 2 intraspecific interactions and 3 interspecific interactions versus 60 single-species flocks with 2 intraspecific interactions, makes it difficult to detect broad tendencies, but we found no significant increase in agonistic encounters for Prothonotary Warblers in mixed-species flocks. Although we did not examine food availability, it could be that the relatively moist conditions present in the mangrove over the winter supported sufficiently large arthropod populations so that food was not limiting. In terms of predation risk, all individuals in a mixed-species flock should benefit from auditory predator warnings regardless of species (Hutto 1994), and thus the larger mixed-species flocks we observed should be afforded greater predator protection. Yet mixed-species flocks were not the most common foraging association involving Prothonotary Warblers that we encountered. Perhaps predation is not a strong selective pressure in the region. Although Ferruginous Pigmy-Owls (*Glaucidium brasilianum*), Sharp-shinned Hawks (*Accipiter striatus*), and Peregrine Falcons (*Falco peregrinus*) were seen at Tivives, we have no detailed data on the survivorship of wintering warblers at this site.

To fully understand the factors influencing foraging decisions for the Prothonotary Warbler and other species that may forage alone, in single-species flocks, or in mixed-species flocks, more detailed studies of marked individuals foraging in each of these three situations are needed. Although we color-marked Prothonotary Warblers, we were unable to collect any significant amount of foraging data for the same individual in different flocking situations. Such data would be invaluable in assessing more effectively the impact which flock composition and size have upon foraging behavior.

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MORPHOLOGICAL VARIATION AMONG MIGRATORY AND NON-MIGRATORY POPULATIONS OF PRAIRIE WARBLERS

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ABSTRACT.—The two subspecies of Prairie Warblers (*Dendroica discolor*) differ in migratory behavior and habitat use. A concurrent study of mitochondrial DNA variation showed that behavioral differences between subspecies may persist because little gene flow occurs between subspecies. To determine whether geographic variation in morphology parallels variation in migratory behavior and mitochondrial DNA, I used measurements of museum specimens from throughout the Prairie Warbler's range. The subspecies differ in overall body size, with birds of the Florida subspecies (*D. d. paludicola*) significantly larger than the nominate race. Males of the subspecies differ in the extent of white coloration in the outer rectrices. These differences were apparent even among specimens collected in northern Florida and southern Georgia, where the subspecies' ranges are most proximate. Morphological differences coincide with differences in behavior and mitochondrial DNA and support the recognition of migratory and non-migratory forms of Prairie Warblers as subspecies and as potentially independent evolutionary lineages. *Received 21 May 1999, accepted 23 Oct. 1999.*

Prairie Warblers (*Dendroica discolor*) consist of two geographically separated subspecies that differ in migratory behavior and habitat use (Nolan 1978). One subspecies (*D. d. discolor*) is migratory between its breeding range in the eastern United States (south to northern Florida) and its winter range in Florida and the West Indies (Nolan 1978). *Dendroica d. discolor* is a habitat generalist and is found in southern pine (*Pinus*) forests, forest-grassland edges, abandoned fields, dunes, and other early successional habitats (Nolan 1978). The other subspecies (*D. d. paludicola*) is non-migratory and is restricted throughout the year to mangroves in subtropical Florida (Robertson and Woolfenden 1992, Stevenson and Anderson 1994).

Because the geographic distribution of heritable phenotypic variation is in part determined by underlying patterns of gene flow, discontinuous variation is usually restricted to interspecific differences, whereas intraspecific geographic variation is more commonly continuous and expressed as a cline (Zink and Remsen 1986). Given previous demonstrations of significant genetic contributions to inter-population differences in migratory behavior (Berthold and Helbig 1992), the geographic distribution of migratory and non-migratory Prairie Warblers suggests that there is little gene flow between *D. d. discolor* and *D. d. paludicola.* Limited gene flow across the relatively small distance (ca 200 km) separating the breeding ranges of two subspecies would be surprising given the capacity for long distance movements by Prairie Warblers and the observation that some *D. d. discolor* migrate to Florida for the non-breeding season (Stevenson and Anderson 1994). On the other hand, genetic isolation might be expected based on the disparate breeding habitats used by the two subspecies.

In a concurrent study of the distribution of mitochondrial (mt) DNA variation, I found evidence for reduced gene flow, but no well supported phylogenetic distinction between the subspecies (Buerkle 1999). Ideally, multiple independent genetic loci would be used to address this question. However, in the absence of additional genetic data, morphology can provide "surrogate genetic information" to studies of intraspecific phylogeny and geographic variation (Avise 1994:242). The use of morphological characters requires consideration of environmental influences on development, but morphological variation may reflect underlying genetic variation (e.g., Boag 1983). Substantial differences in morphology between migratory and non-migratory Prairie Warblers would be consistent with an interruption of gene flow between *D. d. discolor* and *D. d. paludicola.* Because they may have different evolutionary histories, it is not necessary that all three classes of characters (morphological, genetic, and behavioral) co-

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FIG. 1. Geographic regions used to pool (a) male and (b) female specimens. Shades of gray are used to differentiate adjacent regions. States without shading are not represented in this study. Number of male specimens from each region (in ascending numerical order): 19, 20, 8, 13, 16, 17, 12, 16, 23, 13, 10, 8, 27. Number of female specimens from each region (in ascending numerical order): 8, 8, 5, 9, 11, 8, 11.

vary geographically. However, concordance among them would support the hypothesis that despite their geographic proximity, migratory and non-migratory subspecies of Prairie Warblers are isolated from one another and may continue to diverge.

Previous descriptions of the morphology of Prairie Warbler subspecies have not identified any plumage or other morphological characters that can be reliably used to identify subspecies (see Howell 1930, Nolan 1978). Howell's (1930) description of *D. d. paludicola* is generally consistent with the morphology of many individuals of *D. d. discolor,* and it is possible that he recognized the Florida Prairie Warbler as a separate subspecies based partially on its unusual breeding habitat. Howell (1930) referred to *D. d. paludicola* as a common breeder and did not mention the subspecies' migratory status.

In this paper I describe morphological variation among populations of Prairie Warblers, with the goal of determining whether the geographic distribution of morphological variation is coincident with the difference in migratory behavior and mtDNA variation. I used morphological data obtained from measurements of Prairie Warbler specimens in museum collections to determine the pattern of geographic variation. In particular, I used multivariate analyses to evaluate the distinctiveness of the Florida subspecies and to determine whether the pattern of morphological variation offers additional evidence for a reduction of gene flow between *D. d. paludicola* and *D. d. discolor.*

METHODS

From the collections of nine institutions (see Acknowledgments), I selected specimens collected between 1 May and 31 August, 1869–1989. Specimens available from Florida were collected between 6 May and 23 June. A small number of the birds at the extremes of the 1 May to 31 August period may have been migrants; however, based on dates of migration from Nolan (1978), this sample should contain primarily breeding residents. Error introduced by migrants would tend to obscure variation among locations.

In selecting specimens I gathered birds collected from locations across the range of the species, which I then grouped into general geographic regions. It would be preferable to have a number of specimens from single locations (i.e., point samples); however, this was not possible with existing specimens. Because of known sexual dimorphism (Nolan 1978, and confirmed with these specimens), I considered females and males separately. Collections contained far fewer female specimens than male, therefore I used separate schemes for defining geographic regions for males and females. While attempting to minimize the size of regions, I grouped specimens into regions so that each region contained approximately 10 or more specimens and roughly equal numbers of individuals. Specimens were first grouped by state in which they were collected; then adjacent states with fewer than 10 specimens were pooled (Fig. 1). This method of pooling

TABLE 1. Character correlation matrix for males (below diagonal) and females (above diagonal).

	Bwidth	Eculmen	Culmen	Rectrix4	Rectrix5	Rectrix6	Tail	Tarsus	Toe	Wing
Bwidth	—	0.476	0.313	0.224	0.060	0.203	0.258	0.387	0.391	0.217
Eculmen	0.340	—	0.730	−0.002	−0.034	−0.040	0.158	0.427	0.368	0.127
Culmen	0.400	0.646	—	−0.047	−0.079	−0.089	0.295	0.323	0.323	0.134
Rectrix4	0.064	0.074	0.045	—	0.644	0.430	0.285	0.208	0.078	0.402
Rectrix5	0.057	0.012	0.081	0.735	—	0.547	0.324	0.224	0.330	0.434
Rectrix6	0.084	0.089	0.114	0.518	0.708	—	0.383	0.183	0.244	0.109
Tail	0.143	0.201	0.324	0.172	0.189	0.220	—	0.392	0.559	0.585
Tarsus	0.153	0.243	0.168	−0.103	−0.076	0.077	0.252	—	0.531	0.318
Toe	0.174	0.265	0.263	−0.049	−0.049	0.037	0.307	0.469	—	0.484
Wing	0.058	−0.003	0.134	0.359	0.340	0.324	0.458	0.123	0.090	—

specimens is conservative and any error will tend to obscure variation among locations.

The sex of specimens was taken from museum tags and confirmed using criteria based on plumage coloration in Nolan (1978). These were rarely in disagreement. Based on plumage coloration, a few specimens were obviously not the sex they had been labeled, and in these cases I relied on plumage criteria in Nolan (1978) for determining sex. I distinguished between hatching-year birds (in first basic plumage and prior to 31 December) and after-hatching-year birds (birds in at least their second calendar year) based on plumage characteristics (Nolan 1978). Very few hatching-year birds were available and the analysis below is of after-hatching-year birds only.

I measured 11 characters on study skins: (1) Wing, wing chord length of unflattened wing from anterior bend in the wing to tip of longest primary; (2) Tail, length of central rectrices from insertion point to tip; (3) Bdepth, depth of bill measured from upper to lower mandible at anterior edge of the nares; (4) Bwidth, width of bill measured at anterior edge of the nares; (5) Eculmen, chord length of exposed culmen measured along bill axis from the edge of feathering at base of bill to tip of upper mandible; (6) Culmen, chord length of bill from anterior edge of nares to tip of the upper mandible; (7) Rectrix4, length of white area along rachis of fourth rectrix (rectrix otherwise blackish); (8) Rectrix5, length of white on fifth rectrix; (9) Rectrix6, length of white on sixth (outermost) rectrix; (10) Tarsus, tarsus length measured diagonally from the posterior surface of the metatarsus to the anterior margin of the last scute on the metatarsus; (11) Toe, length of hind toe including claw, from base on dorsal surface of the digit to tip of claw (terminology follows Zink 1986, Pyle et al. 1987, Atwood 1988). All of these, except for tail length, were measured with digital calipers and recorded to the nearest 0.01 mm. I measured tail length with a ruler inserted between central rectrices and recorded values to the nearest 0.5 mm. (Univariate descriptive statistics and numbers of individuals measured for each character are available from the author upon request.)

I did not measure all characters for specimens with features that were either missing or damaged, and I did not measure heavily damaged specimens. Otherwise, all specimens were measured and included in the analysis. Out of 269 specimens, 1 had six missing characters, 4 had four missing characters, and 2 had three missing characters; all others had two or fewer missing

TABLE 2. Loading of variables on first five principal components for males. Eigenvalues, percentage of variation accounted for by each principal component, and the cumulative percentage of variation explained.

	PC1	PC2	PC3	PC4	PC5
Bwidth	0.388	0.390	−0.411	−0.017	0.721
Eculmen	0.465	0.560	−0.437	0.038	−0.342
Culmen	0.544	0.530	−0.396	−0.213	−0.219
Rectrix4	0.626	−0.560	−0.140	0.105	−0.027
Rectrix5	0.674	−0.600	−0.117	0.200	−0.023
Rectrix6	0.680	−0.432	−0.027	0.299	−0.026
Tail	0.610	0.191	0.391	−0.442	−0.070
Tarsus	0.311	0.510	0.479	0.415	0.088
Toe	0.356	0.544	0.399	0.334	−0.034
Wing	0.586	−0.205	0.397	−0.474	0.130
Eigenvalue	2.910	2.241	1.251	0.891	0.717
% of Variance	29.1	22.4	12.5	8.9	7.2
Cum. % of Var.	29.1	51.5	64.0	72.9	80.1

TABLE 3. Loading of variables on first five principal components for females. Eigenvalues, percentage of variation accounted for by each principal component, and the cumulative percentage of variation explained.

	PC1	PC2	PC3	PC4	PC5
Bwidth	0.577	0.303	0.400	−0.096	−0.514
Eculmen	0.507	0.692	0.280	0.182	0.151
Culmen	0.458	0.683	0.076	0.225	0.425
Rectrix4	0.513	−0.564	0.330	0.446	−0.080
Rectrix5	0.568	−0.633	0.118	0.149	0.177
Rectrix6	0.474	−0.521	0.391	−0.446	0.265
Tail	0.740	−0.105	−0.378	−0.161	0.179
Tarsus	0.685	0.222	0.017	−0.163	−0.203
Toe	0.757	0.153	−0.297	−0.320	−0.043
Wing	0.669	−0.199	−0.501	0.346	−0.181
Eigenvalue	3.647	2.150	1.002	0.788	0.683
% of Variance	36.5	21.5	10.0	7.9	6.8
Cum. % of Var.	36.5	58.0	68.0	75.9	82.7

characters. Bill depth was not used in the multivariate analyses because it was missing from 21.3% of females and 24.5% of males. Observations for other characters were missing from less than 5% of individuals.

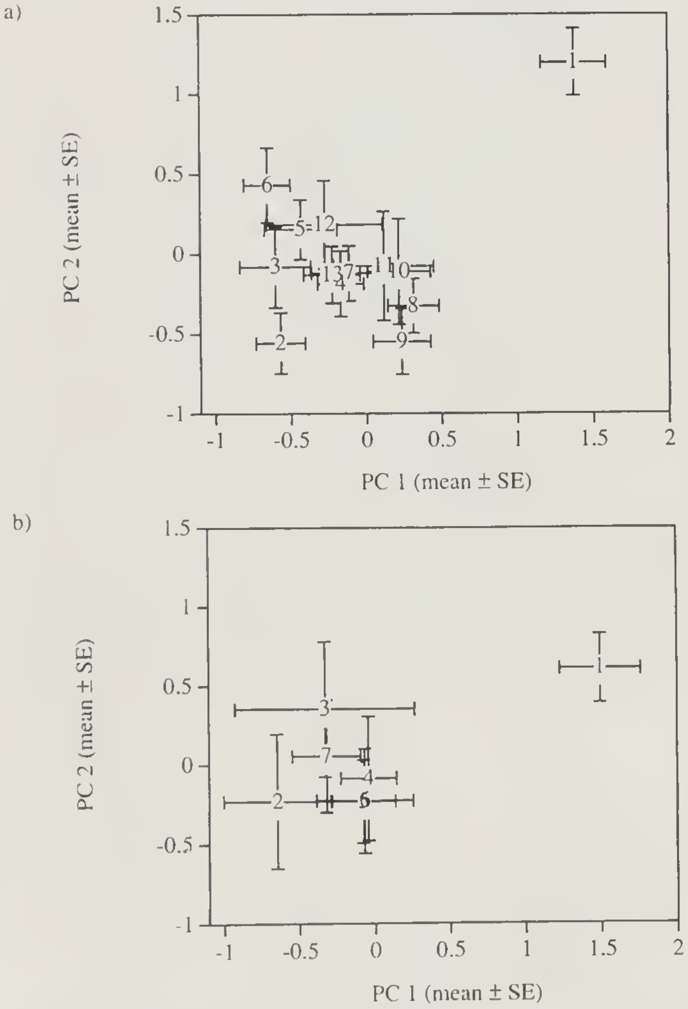

FIG. 2. Plots for (a) males and (b) females of PC1 versus PC2 for region means (± SE). Numbers used to identify regions are the same as in Fig. 1. Labels for regions 5 and 6 overlap in the plot for females.

I used principal components analysis (PCA) to extract a limited number of independent variables from the measured characters (FACTOR procedure; SPSS version 6.1 for Macintosh; SPSS Inc. 1995). In calculating principal components, I substituted the grand mean for missing characters. This procedure is conservative in that it will tend to reduce variation among populations; yet it allowed me to include information from a greater number of specimens. Using principal component scores as the dependent variable, I performed an analysis of variance (ANOVA) to test for variation among regions (ONEWAY procedure; SPSS Inc. 1995). I also performed two planned comparisons to test for the distinctiveness of Florida Prairie Warblers: Florida mean versus the average of the means of all other regions, and Florida mean versus Georgia mean (CONTRAST procedure; SPSS 1995).

RESULTS

Several of the measured characters were highly correlated, while others were not (Table 1). Principal Components Analysis resulted in three factors with eigenvalues greater than one (Tables 2, 3), and only these are considered here because the remaining factors explained less of the variation among individuals than did the individual original variables (Norusis 1994). The first three PC factors together explained 64% and 68% of the total variance for males and females, respectively.

All measured variables were positively correlated with PC1 for both males and females, suggesting that PC1 corresponds to overall body size (Tables 2, 3). The contribution of various characters to PC2 differed between males and females (Tables 2, 3). For males, large positive values for PC2 corresponded to small amounts of white in the rectrices (Rec-

TABLE 4. ANOVA and planned comparison results for principal component scores for males. Regions refer to geographic regions described in Fig. 1. Planned comparisons utilize separate variance estimates and an approximate *t*-test (Lindman 1992). ω^2 refers to the proportion of total variation that is accounted for by differences between regions.

Source	df	MS	*F*	*P*	ω^2_{bet}
PC1					
Between Regions	12	5.150	7.120	<0.001	0.267
Within Regions	189	0.723			
Total	201				
	t	df	*P*		
Florida vs Other	6.930	21.7	<0.001		
Florida vs Georgia	7.213	34.1	<0.001		
	df	MS	*F*	*P*	ω^2_{bet}
PC2					
Between Regions	12	3.927	4.987	<0.001	0.192
Within Regions	189	0.788			
Total	201				
	t	df	*P*		
Florida vs Other	5.954	22.0	<0.001		
Florida vs Georgia	6.187	36.5	<0.001		
	df	MS	*F*	*P*	ω^2_{bet}
PC3					
Between Regions	12	3.623	4.324	<0.001	0.165
Within Regions	189	0.838			
Total	201				
	t	df	*P*		
Florida vs Other	1.06	23.7	0.300		
Florida vs Georgia	2.67	36.8	0.011		

trix4–Rectrix6) and large dimensions for all other variables except for wing length (Table 2). Negative values for PC2 corresponded to larger amounts of white in the tail and smaller overall body proportions (except for Wing). Similarly, for females the amount of white in the rectrices (Rectrix4–Rectrix6) was highly negatively correlated with PC2, bill dimensions were highly correlated positively, and other dimensions had smaller correlations with PC2 (Table 3). For males, bill dimensions were negatively correlated with PC3 and four other variables (Tail, Tarsus, Toe, Wing) were positively correlated (Table 2). For females, wing, toe, and tail lengths were negatively correlated with PC3 and other dimensions had either low or positive correlations (Table 3).

Bivariate plots of regional means for principal component scores suggested that birds from Florida (Region 1) were distinct from those from the remaining regions (Fig. 2). The disjunction was evident on both PC1 and PC2 for males, whereas females from Florida appeared to differ from the remaining regions only on PC1. The obvious graphical differences on PC1 and PC2 for males, and on PC1 for females, were statistically significant in the analysis of variance and planned comparisons (males: Table 4; females: Table 5). According to the differences on PC1, *D. d. paludicola* males and females generally are larger than *D. d. discolor* individuals. On the second PC axis Florida males had the largest positive scores ($\bar{x} = 1.19$, Fig. 2a), indicating that Florida males had less white in their tails relative to their overall body size. In comparison, *D. d. discolor* males had smaller scores (range of means: −0.56–0.42), that are indicative of a smaller disparity in the amount of white relative to body size. For females, less of the variation in PC2 was associated with differences among regions and only the comparison

TABLE 5. ANOVA and planned comparison results for principal component scores for females. Regions refer to geographic regions described in Fig. 1. Planned comparisons utilize separate variance estimates and an approximate *t*-test (Lindman 1992). ω^2 refers to the proportion of total variation that is accounted for by differences between regions.

Source	df	MS	*F*	*P*	ω^2_{bet}
PC1					
Between Regions	6	3.831	5.485	<0.001	0.310
Within Regions	53	0.698			
Total	59				
	t	df	*P*		
Florida vs Other	−5.777	11.1	<0.001		
Florida vs Georgia	−4.822	13.0	<0.001		
Source	df	MS	*F*	*P*	ω^2_{bet}
PC2					
Between Regions	6	0.848	0.819	0.560	0
Within Regions	53	1.035			
Total	59				
	t	df	*P*		
Florida vs Other	−2.518	14.6	0.024		
Florida vs Georgia	−1.763	10.5	0.107		
Source	df	MS	*F*	*P*	ω^2_{bet}
PC3					
Between Regions	6	1.511	1.738	0.130	0.069
Within Regions	53	0.870			
Total	59				
	t	df	*P*		
Florida vs Other	0.232	8.5	0.822		
Florida vs Georgia	0.774	12.4	0.453		

of PC2 means between Florida and all other regions pooled was significant (Table 5).

Similar plots of regional means for PC2 and PC3 indicated that for PC3 the Florida means for males and females fell within the range of means from the other regions (Fig. 3). Means for male specimens on PC3 did not differ between Florida and all other regions pooled, but the Florida mean was different from the Georgia mean (Table 4). For females, none of the comparisons involving PC3 was significant (Table 5).

DISCUSSION

Morphological differences between *D. d. paludicola* and *D. d. discolor* parallel differences in behavior (migratory tendency and habitat use) and mtDNA (Buerkle 1999). With respect to avian taxonomy, the observed morphological differences are consistent in magnitude with those between typical avian subspecies (Morrison 1983, Ball and Avise 1992). However, the concordance among independent classes of characters suggests that *D. d. paludicola* and *D. d. discolor* may represent relatively distinct evolutionary lineages that harbor disparate evolutionary potentials and may continue to diverge over time. This study and others (e.g., Avise and Nelson 1989, Rising and Avise 1993) demonstrate that significant boundaries among populations of birds are not necessarily associated with obvious geographic barriers to dispersal, and that morphological differences may be cryptic and need not include plumage differences that are easily observed by humans.

The two primary differences found in the PCA can be summarized as follows: Florida Prairie Warblers are larger than *D. d. discolor* individuals, and males of *D. d. paludicola* have less white in the tail. The functional aspects of the size difference may be related to both migratory behavior and habitat use because these behaviors may constrain one an-

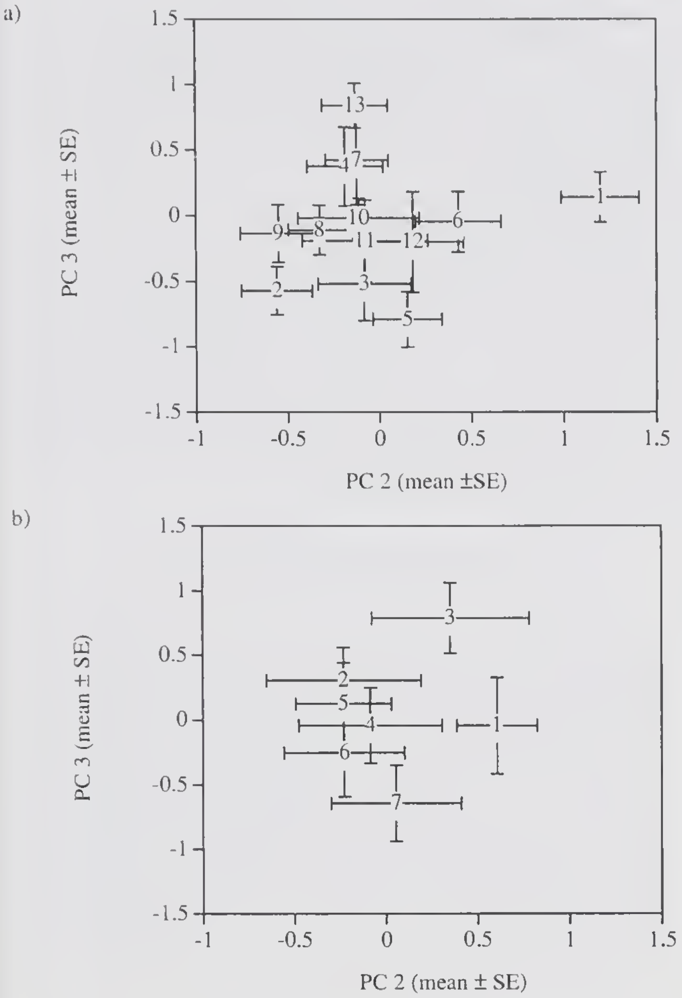

FIG. 3. Plots for (a) males and (b) females of PC2 versus PC3 for region means (± SE). Numbers used to identify regions are the same as in Fig. 1.

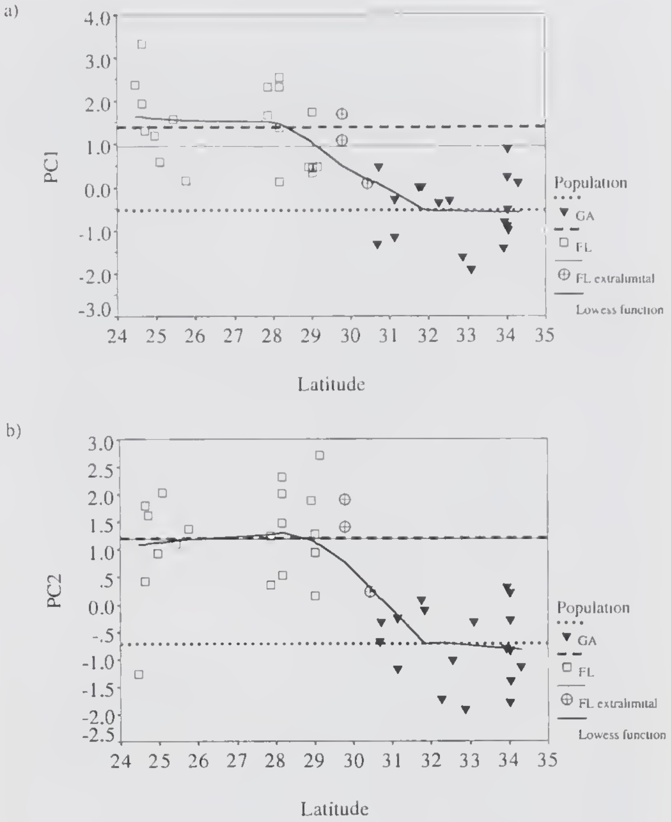

FIG. 4. Plots of (a) PC1 and (b) PC2 versus latitude for male specimens from Florida and Georgia. Horizontal lines indicate group means. Lowess line is based on a locally weighted least squares regression (local fit of line to 50% of data points; SPSS Inc. 1995). Latitude data were obtained by using locality information on museum tags and the Geographic Names Information System of the United States Geological Survey. Specimens with ambiguous locality information were excluded. Three Florida specimens from outside the known range of *D. d. paludicola* are coded as FL extralimital.

other through morphology (Winkler and Leisler 1992). Migration distance is positively correlated with wing length in parulids (Parulidae including *Dendroica*; Winkler and Leisler 1992), as is openness of habitat (or vegetation height) in Old World warblers (Sylviidae) and other avian families (Zink and Remsen 1986, Winkler and Leisler 1992). Although a trend for increasing wing length with latitude and migration distance was evident (unpubl. data), this does not explain the overall larger size of *D. d. paludicola.* It is possible that differences between subspecies are related to differences in migratory behavior and habitat use, but an understanding of that relationship requires further study.

The difference between male *D. d. paludicola* and *D. d. discolor* in the amount of white in the tail may be related to the potential role of the tail, and particularly the conspicuous white area, in intra- and intersexual behavior (Nolan 1978). Prairie Warblers commonly fan their tails in display flights during territorial encounters and courtship (Nolan 1978); differences in the function or performance of either type of behavior could result in morphological divergence. In interpreting the functional significance of morphological differences described here, it must be kept in mind that the analysis is a fairly limited description of Prairie Warbler morphology. The limited number of variables I measured served the purpose of differentiation between taxa. However, their utility for understanding the possible role of selection in shaping differences is limited. Detailed study of behavioral and habitat differences might indicate which morphological variables should be compared to better understand the potential role of adaptation.

One striking feature of the comparisons of regional means is the difference between the

Florida and Georgia populations (Fig. 2). In addition to the differences in means between birds from Georgia and Florida, there is generally little overlap of the principal component scores of individual male specimens from these regions (Fig. 4). The differences in means between regions are evident even among individuals separated by approximately 200 km. Included in Fig. 4 are three specimens from locations in Florida that lack mangroves typical of peninsular Florida (Tallahassee, coastal Dog Island south of Tallahassee). The two specimens from Dog Island (upper two on PC1 and PC2; Tall Timbers Research Station specimens #2895 and #2897) were collected in mid-June eleven years apart and may represent *D. d. paludicola* vagrants along the Gulf Coast. Dog Island supports an isolated, stunted black mangrove (*Avicennia germinans*) community, not the typical mangrove communities along the peninsular Gulf Coast, which are more diverse and consist of taller trees (Sherrod and McMillan 1983). Because the Dog Island specimens were missing data for the white in the tail (Rectrix4–Rectrix6), their affinity to either group was not tested with discriminant function analysis. The specimen from Tallahassee (Smithsonian Institution #599804) was probably a migrant. It was killed by a nocturnal collision with a television tower (1 May) and had a large amount of subcutaneous fat.

Because of its rarity and restricted range, the status of *D. d. paludicola* populations is of concern (Florida Natural Areas Inventory 1995). Evidence for the morphological distinctiveness of *D. d. paludicola*, along with divergent behavior and genetics, suggests that the two Prairie Warbler subspecies are likely to have distinct evolutionary potentials. Recognition of such evolutionarily significant units can aid in defining conservation priorities (Moritz 1994, Lesica and Allendorf 1995). Suitable habitat for *D. d. paludicola* is very limited because populations are restricted to mangroves and do not breed inland (Robertson and Woolfenden 1992, Stevenson and Anderson 1994). In addition, land development has substantially reduced or modified mangrove habitat with 90% of the remaining acreage in the four southernmost counties in the state (Gilmore and Snedaker 1993). Given that Florida Prairie Warblers are one of very few land birds that breed in mangroves (Robertson 1955, Robertson and Kushlan 1974), their status should be considered when evaluating acquisitions of mangrove habitat for protection.

The substantial discontinuity between birds of Florida and of the remaining regions is the most conspicuous feature of geographic variation in Prairie Warbler morphology. The results support previous taxonomic recognition of *D. d. paludicola* and *D. d. discolor* as subspecies and suggest the potential for further evolutionary divergence.

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MACRO-HABITAT FEATURES ASSOCIATED WITH PAINTED AND INDIGO BUNTINGS IN NORTHEAST TEXAS

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ABSTRACT.—Habitat features found within 4.1 ha sample areas surrounding the song perches of 33 Indigo Buntings (*Passerina cyanea*) and 33 Painted Buntings (*Passerina ciris*) in northeast Texas were compared to determine whether these species segregated according to habitat. The species did not differ in the proportions of open habitat or the type and amounts of successional and mature woodland in the sample areas surrounding their song perches. Indigo Buntings were mostly associated with lower elevations where they occurred along the edges of successional and mature woodlands. Painted Buntings showed no elevation bias. Compared to Indigo Buntings, Painted Buntings were associated with smaller, more numerous, and more heterogeneous stands of trees. In general, Indigo Buntings typically occurred where there were open areas within otherwise wooded habitats whereas Painted Buntings tended to occur where there were wooded areas in otherwise open habitat. *Received 17 June 1999, accepted 28 Sept. 1999.*

Indigo Buntings (*Passerina cyanea*) are a familiar passerine that breed through much of North America east of the Great Plains. In central and west Texas, they are largely replaced by the congeneric Painted Bunting (*Passerina ciris*; Sauer et al. 1997). However, there is a broad zone of overlap between these two species extending across much of Oklahoma, east Texas, and Louisiana where both are equally abundant (Sauer et al. 1997).

The habitats of both Indigo and Painted buntings are described in the popular literature as brushy areas, river and streamside thickets, and forest edges (Peterson 1947, Robbins et al. 1983). However, Parmelee (1959) observed that Painted and Indigo buntings were seldom observed in the same areas in Oklahoma. This suggests that, at least where these buntings are sympatric, the two species might occupy different habitats.

Taber and Johnston (1968) provided a qualitative overview of the habitats frequented by Indigo Buntings, but there are no studies quantifying the habitats of this species (Payne 1992). However, Indigo Buntings appear in a number of studies on avian community associations relative to habitat features (Posey 1974, Conner et al. 1983, Yahner 1986, Best et al. 1995), ecological gradients (Johnston and Odum 1956, Shugart and James 1973), and habitat alteration (Stauffer and Best 1980, Strelke and Dickson 1980, Triquet et al. 1980, Yahner 1993). Thus, albeit indirectly, the breeding habitat of the Indigo Bunting has been well documented through many portions of its geographic distribution. On the other hand, there is little quantitative data on habitat features associated with Painted Buntings (Lowther et al. 1999). A single quantitative study of Painted Bunting breeding habitat was conducted at the northern edge of the species' distribution in Missouri (Norris and Elder 1982). In addition, there are three qualitative descriptions: one by Parmelee (1959), a second by Sprunt (1968), and a third by Lowther and coworkers (1999). Painted Bunting habitats are cursorily identified in three avian community studies; two in southeast Texas (Dickson and Segelquist 1979, Dickson et al. 1995) and one near the periphery of the species' distribution in northwest Arkansas (Shugart and James 1973). There is no information on whether sympatric populations of Indigo and Painted buntings are ecologically segregated relative to habitat.

The objective of our study was to provide a quantitative description of Indigo and Painted bunting habitat in northeast Texas by evaluating macro-habitat features around the song perches of territorial males and to test the hypothesis that, in northeast Texas, Indigo and Painted buntings are segregated according to habitat.

METHODS

Study area.—The study was conducted on the agricultural property of Texas A&M University–Commerce adjacent to the city of Commerce (33° 15′ N, 95° 55′ E) in Hunt Co., Texas. The study area consisted

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of 5.5 km^2 of land that varied considerably in elevation and habitat types, but which reflected variation typical of this region. About 60% of the area consisted of managed and unmanaged pasture interspersed with wooded streamsides, bottomland woods, upland woods, and fencerows. The woody vegetation in these pastures varied considerably and contained a wide variety of secondary and mature growth. Cropland, active and idle, accounted for about 15% of the area. These fields contained no woody vegetation but were often bordered by shrubby fencerows. About 10% of the area was managed and unmanaged hay fields. These areas were bounded by shrubby fencerows and, in one case, contained a streamside thicket and isolated stands of trees. The rest of the study area was bottomland woods and idle land in various stages of succession. Dominant trees on the study area were black oak (*Quercus velutina*), hickory (*Carya* spp.), green ash (*Fraxinus pennsylvanica*), sugarberry hackberry (*Celtis laevigata*), pecan (*Carya illinoensis*), cedar elm (*Ulmus crassifolia*), osage orange (*Maclura pomifera*), honey locust (*Gleditsia triacanthos*), post oak (*Quercus stellata*), red cedar (*Juniperus virginiana*), plum (*Prunus* spp.), and persimmon (*Diospyros virginiana*).

The topography varied from level to slightly rolling. Several drainages ran through the area with intermittent creeks on upland sites and permanent creeks in bottomland areas. A small river, the South Sulphur River, ran through the middle of the study area. In addition, several stock ponds were distributed throughout. Drainages were typically lined with scrubby trees in upland sites and larger, thicker woods in bottomland areas. Mature bottomland woods grew along the South Sulphur River.

Data collection and analyses.—Song perches were located between 06:00 and 12:00 from 5 May 1996 through 25 June 1996 and were plotted onto maps of the study area. The song perches used for analysis were always the first perch from which an individual was observed singing. Subsequently, we used spot-mapping (Robbins 1970) to discriminate the owners of the perches and to verify that adjacent song perches represented different individuals. Spot mapping can cause some individuals to be overlooked while others are duplicated (see review in Verner 1985). We were most concerned with the latter type of error and took measures to eliminate the duplication of individuals in the sample. When a song perch was identified, we also plotted the locations of immediate neighbors. These simultaneous registrations (Robbins 1970) ensured that adjacent song perches did not belong to the same individuals. Furthermore, Painted Buntings do not share song types with neighbors (Forsythe 1974). We found that some individuals could be individually recognized as did Forsythe (1974) in South Carolina and Georgia. By carefully noting songs, we could relocate specific individuals. We made at least three visits to each song perch to verify the locations of its owner and his neighbors. By using a combination of simultaneous registrations, recognition of individuals when possible, and by corroborating multiple observations of singing males with the locations of specific song perches, we felt confident that all the song perches used were by different individuals. Song perches of 33 Indigo and 33 Painted buntings were identified.

Habitat features surrounding the song perches were quantified using aerial photographs obtained from the U.S. Geological Survey. Song perch locations were transcribed onto stereoscopic pairs of photographs enlarged to a scale of 1:8000 (1.0 cm = 80 m), and a 229 m diameter circular plot (area = 4.1 ha) was used to define a sampling area around each song perch. To establish the diameter of this sample area the average nearest neighbor distances were first calculated for each species. These distances did not differ between species (Indigo Bunting $\bar{x} \pm$ SD = 217 ± 159 m; Painted Bunting = 240 ± 195 m; t-test: $t_{64} = 0.52$, $P > 0.05$). Therefore, we used the overall average nearest neighbor distance of the two species (229 m) as the diameter of the sample area.

Habitat features were identified on the photographs and outlined on transparent overlays. Because the USGS photographs were taken in 1989, the features identified had to be verified by ground surveys. In particular, we verified the locations and sizes of fence rows, isolated trees, stands of trees, and the borders of larger wooded areas. We compensated for changes in the condition of open habitats caused by changes in land use. The data were grouped into three broad categories. Variables that measured vegetation type and successional stage included open habitat, which contained less than 10% coverage by woody vegetation, and wooded habitats, which contained more than 90% coverage by woody vegetation. Wooded habitats were divided into early successional woods, late successional woods, and mature woods. Variables reflecting habitat heterogeneity included the number of isolated trees, the number of stands of trees, the size of the largest open area, the size of the largest stand of trees, the length of edge around the largest stand of trees, and the percent of wooded areas composed of even-aged stands. Physiographic variables were the presence of water, creeks, creek beds, elevation, and type of slope.

Open habitats were areas dominated by grasses, forbs, or both. Early successional vegetation were areas that, on the 1989 photographs, were open, but which in 1996 were colonized by woody vegetation. Stereoscopic imaging allowed vegetation height to be easily estimated. As a result, late successional vegetation could be identified as could the presence and distribution of even-aged stands. The number of stands included all wooded areas bounded by open vegetation and included fencerows and isolated trees. Aquatic habitats consisted of intermittent creeks, permanent creeks, and permanent ponds. Elevation was determined by plotting the song perches onto USGS topographic maps (scale 1:24,000) and interpolating between contour intervals (contour interval was 10 ft). Values were read in ft and subsequently converted to m. Slope was categorized according to whether the

TABLE 1. Area occupied (%) by open habitat, successional woody vegetation, and mature woods for sample areas surrounding the song perches of Indigo and Painted buntings.

Measure	Indigo Bunting Mean ± SD	Painted Bunting Mean ± SD	P[a]	Adjusted α[b]
% Open	48.91 ± 16.81	49.67 ± 23.60	0.787	0.050
% Early 2nd growth	16.12 ± 9.21	11.70 ± 10.25	0.012	0.013
% Late 2nd growth	16.42 ± 7.56	16.58 ± 11.42	0.381	0.025
% Mature forest	16.00 ± 8.10	13.88 ± 9.37	0.212	0.030

[a] Probabilities based on Wilcoxon's Rank-Sum Tests, $n = 33$ for each species.

[b] Adjusted values of α needed to reject the null hypothesis based on the sequential Bonferroni method (Rice 1989). Experiment-wise error was set at 5%.

song perch occurred within the top half of a slope, the bottom half of a slope, or on level ground.

The data were analyzed using SAS Release 6.12 on a Windows 95 based computer. The variables were found to be non-normally distributed using Wilk's Statistic (all $P > 0.05$; SAS Institute Inc. 1990); therefore, Wilcoxon's Rank Sum Tests were used for comparisons between species (Pratt and Gibbons 1981). Two variables, types of aquatic habitats present and type of slope, were categorical and were analyzed using χ^2 multiway contingency tables (Model II; Sokal and Rohlf 1995). To test whether the two bunting species were randomly distributed relative to available elevations, the elevation data were stratified into five equal-sized elevation classes. Pearson's χ^2 was then used to test the null hypothesis that the buntings occupied each class with equal frequency.

Because a large number of univariate comparisons were involved in the analyses, the sequential Bonferroni technique was used to adjust the value of α (α_{adj}) necessary to reject the null hypothesis of no difference between species (Rice 1989, Sokal and Rohlf 1995). Based on the discussion by Chandler (1995) we applied this adjustment separately to three families of comparisons that corresponded to the three classes of variables measured; vegetation type, habitat heterogeneity, and physiographic variables. Experimental error was set at 5% for each family of tests (Chandler 1995).

RESULTS

The song perches of both Indigo and Painted buntings were invariably adjacent to edges between open and wooded habitats (all song perches were in trees). Therefore, all of the sample areas contained some wooded habitat and some open habitat. There was no difference between species with respect to the amount of open habitat surrounding the song perches (Table 1) and, by corollary, there was no difference between species in the amount of wooded habitat surrounding their song perches. Similarly, Indigo and Painted buntings did not differ with regard to the presence or amount of early second growth, late second growth, or mature woods (Table 1). There was considerable variation among the individuals of both species as to which vegetation type was dominant within the sample area around the song perch.

Though the two species did not differ in the amount of each vegetation type found around their song perches, there were marked differences in the spatial patterns of these features (Table 2). Thus, while both species occupied sites that contained similar proportions of wooded habitat, Indigo Buntings were associated with fewer isolated trees and fewer stands of trees (Table 2). As a result, the average size of tree stands and the largest tree stand were larger for Indigo Buntings than

TABLE 2. Vegetation variables in sample areas surrounding the song perches of Indigo and Painted buntings.

Measurement	Indigo Bunting Mean ± SD	Painted Bunting Mean ± SD	P[a]	Adjusted α[b]
Number of isolated trees	2.91 ± 5.10	4.30 ± 4.61	0.0155	0.0167
Number of tree stands	5.67 ± 5.78	8.45 ± 5.11	0.0030	0.01
Size of tree stands (m^2)	9119 ± 9032	4040 ± 6093	0.0047	0.0125
Size of largest open area (m^2)	14,004 ± 5782	12,331 ± 5058	0.2637	0.025
Size of largest stand of trees (m^2)	14,706 ± 7436	8723 ± 5132	0.0005	0.0071
Length of edge around largest stand of trees (m)	228.7 ± 54.1	229.5 ± 54.3	0.6572	0.05

[a] Probabilities based on Wilcoxon's Rank-Sum Tests, $n = 33$ for each species.

[b] Adjusted values of α needed to reject the null hypothesis based on the sequential Bonferroni method (Rice 1989). Experiment-wise error was set at 5%.

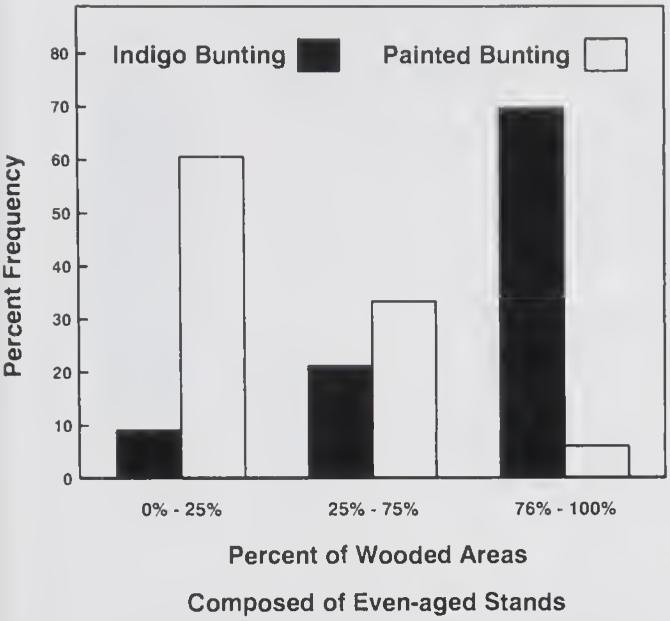

FIG. 1. Presence of even-aged stands of trees surrounding the song perches of Indigo and Painted buntings. Data are expressed in terms of the percentage of stands of trees within the sample areas that were of uniform age.

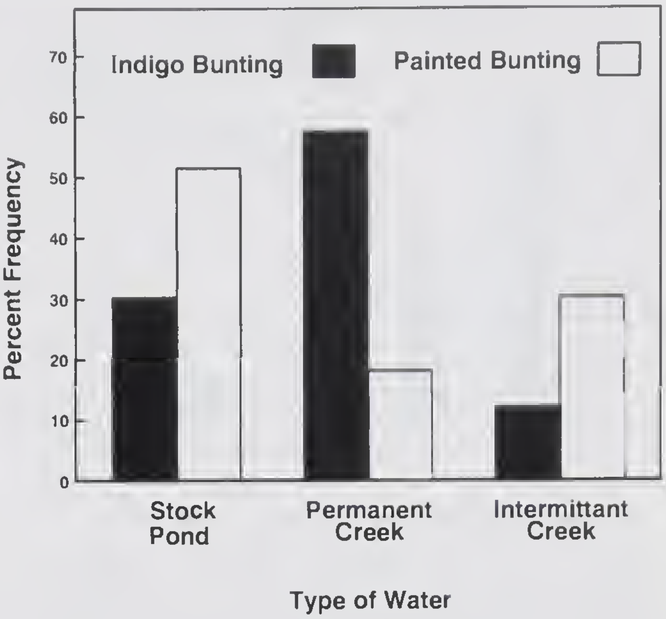

FIG. 2. Types of aquatic habitats found adjacent to the song perches of Indigo and Painted buntings. Permanent creeks always contained water and were found at lower elevations. Intermittent creeks occurred at higher elevations and were often dry.

they were for Painted Buntings (Table 2). However, there was no difference between species relative to the size of the largest open area surrounding their song perches (Table 2).

Given that the largest stand of trees was larger for Indigo Buntings than it was for Painted Buntings, it might be predicted that the edges around these stands should also be longer for Indigo Buntings than for Painted Buntings. Contrary to this expectation, there was no difference between species in the length of edge around the largest wooded area (Table 2). This was because Indigo Bunting song perches frequently occurred on or near linear edges of extensive woodlands. On the other hand, the largest wooded areas associated with Painted Buntings were often irregular clumps of trees or long narrow strips of trees such as those along intermittent streams.

Indigo and Painted buntings also differed relative to the number of even-aged stands of trees surrounding their song perches (Wilcoxon's Rank-Sum Test: $S = 1505.5$, $P = 0.0001$, $\alpha_{adj} = 0.008$; Fig. 1). In this case, the two species exhibited opposing tendencies. For Indigo Buntings, the majority of wooded areas consisted of even-aged stands, whereas for Painted Buntings, the majority of wooded areas were uneven-aged stands (Fig. 1).

Both species tended to be associated with water. For Indigo Buntings 94% of sample areas contained some aquatic habitat, whereas for Painted Buntings, 82% of sample areas contained some aquatic habitat. These percentages did not differ among species (Contingency table: $\chi^2 = 2.28$, df = 1, $P = 0.177$, $\alpha_{adj} = 0.025$). However, the two species differed relative to the type of aquatic habitats present (Contingency table: $\chi^2 = 11.15$, df = 2, $P = 0.005$, $\alpha_{adj} = 0.013$; Fig. 2). Indigo Buntings were more often found near permanent creeks than were Painted Buntings.

Indigo Buntings occurred more frequently at lower elevations than at higher elevations (Pearson's χ^2: $\chi^2 = 22.00$, df = 4, $P = 0.001$, $\alpha_{adj} = 0.01$) whereas Painted Buntings showed no tendency to favor any particular elevation (Pearson's χ^2: $\chi^2 = 2.61$, df = 4, $P = 0.626$, $\alpha_{adj} = 0.05$; Fig. 3). As a result, the song perches of Indigo and Painted buntings differed with respect to elevation (Wilcoxon's Rank-Sum Test: $S = 821$, $P = 0.0003$, $\alpha_{adj} = 0.008$; Fig. 3). There were differences between species in the types of slope on which the song perches occurred (Contingency table: $\chi^2 = 10.40$, df = 2, $P = 0.006$, $\alpha_{adj} = 0.017$; Fig. 4). Thus, while both species most frequently occupied song perches on level ground, when these perches were located on slopes Painted Buntings were more likely to

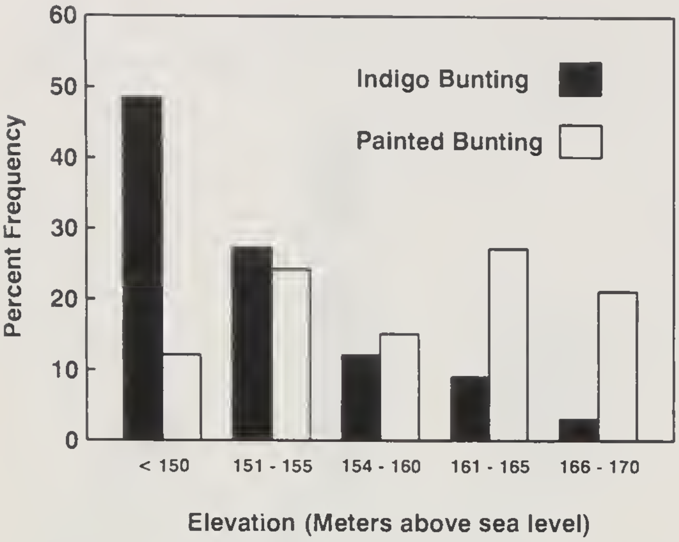

FIG. 3. Surface elevations of Indigo and Painted bunting song perches in meters above mean sea level. The data were stratified into five elevation classes and the bars represent the percent of song perches for each species falling into each elevation class.

FIG. 4. Locations of Indigo and Painted bunting song perches relative to surface inclination.

occur on upper slopes while Indigo Buntings occurred more frequently on lower slopes (Fig. 4).

DISCUSSION

The Indigo and Painted buntings observed in this study occupied a variety of habitats and showed considerable overlap in habitat use. They did not differ relative to vegetation type, successional stage, or the proportion of open and wooded habitat present. However, there were marked differences with respect to habitat heterogeneity. This latter result indicates that the two species are, to some extent, segregated by habitat. Indigo and Painted buntings do not hold interspecific territories (Forsythe 1974); we never observed agonistic interactions between them, and they sometimes sang in the same trees without interaction. Thus, the habitat differences we observed seem to represent differences in habitat selection, although it remains possible that the species exercise passive avoidance.

Indigo Buntings are known to occupy a variety of habitats. In Iowa, they were found in 12 different habitats, ranging from tilled row crops and herbaceous fencerows to upland and bottomland forests (Best et al. 1995). However, in eastern Kansas, Indigo Buntings were more abundant in young forests than in cropland, old fields, or mature hardwood forests (Zimmerman and Tatschl 1975). In northwestern Arkansas, Indigo Buntings preferred xeric forests and woodland edges over old fields, shrubby fields, or mesic forests (Shugart and James 1973). In Wisconsin, Indigo Buntings favored intermediate successional woodlands over pioneer forests or climax forests (Bond 1957). In Illinois, Indigo Buntings were more frequent in early successional shrub habitats than in late successional shrub habitats, bottomland forests, or mature upland forest (Karr 1968). In our study, Indigo Buntings showed a strong affinity for lower elevations and were most often associated with mesic woods and the uniform successional growth typical of moist bottomlands that have been cleared.

Prior to settlement, Indigo Buntings occupied successional habitats and disturbed areas within the continuous eastern forests of North America (Wells 1958). Consequently, they benefit from disturbances that create openings in wooded areas and settle along the edges of agricultural land (Johnston 1947, Warbach 1958, Gates and Gysel 1978) and forest clearcuts (Strelke and Dickson 1980, Yahner 1987, Wigley and Roberts 1994). The Indigo Buntings we observed were no exception. In the bottomlands where they were most frequent, they occurred along edges created by clearing forests for pastures and hay fields.

Painted Buntings also occupied a variety of habitats, but differed from Indigo Buntings in several ways. The most obvious difference was that, while Indigo Buntings usually occurred in openings in otherwise wooded habitats, Painted Buntings were usually found where there were clumps of trees in otherwise open habitat. The wooded patches associated with Painted Buntings were of uneven age and had a high ratio of edge to area. This was because these patches were often long and narrow (fencerows and trees along intermittent streams) or irregular clumps. In the latter case, and in contrast to the abrupt edges associated with Indigo Buntings, these edges were more subtle, natural edges.

Our study site lies on the edge of the post oak savanna ecoregion of Texas (Blair 1950), and the habitat favored by Painted Buntings resembled this environment. Similar environments occur to the north and northeast, where Painted Buntings show similar habitat preferences. In Oklahoma this species is most common in open areas dissected by small stands or strips of trees (Parmelee 1959). In Arkansas, Painted Buntings occupy open areas with clumps of small trees (Shugart and James 1973). However, the distribution of the Painted Bunting includes the southeastern pine forests of Texas and Louisiana, and a disjunct population occurs in the Carolinas, Georgia, and northeastern Florida. In southeast Texas, Painted Buntings are more abundant along narrow strips of mature riparian forest than along medium or wide strips of riparian forest (Dickson et al. 1995), a habitat superficially similar to the one we described. However, in South Carolina, Painted Buntings occur at the interface between coastal forests and salt marshes (Lanyon and Thompson 1986) and along rivers in coastal plain forests (Sprunt 1968), habitats unlike those we described. Therefore, our data on Painted Bunting habitat cannot, without further study, be extrapolated across the distribution of this species, especially in the east. Painted Buntings are Neotropical migrants that have shown significant population declines across their range (Sauer et al. 1997). As a result, there is a strong mandate for further studies on the ecology of this species.

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HENSLOW'S SPARROW HABITAT ASSOCIATIONS ON KANSAS TALLGRASS PRAIRIE

JACK F. CULLY, JR.[1,2] AND HEIDI L. MICHAELS[1]

ABSTRACT.—We examined macro- and microhabitat characteristics of breeding Henslow's Sparrows (*Ammodramus henslowii*) on Fort Riley Military Reservation, Kansas during 1995 and 1996. Survey points were identified at the macrohabitat scale as either grassland, savanna, or woodland edge. A military disturbance index was used to quantify the severity of training disturbance to the vegetation at survey and bird use sites. At the large scale, Henslow's Sparrows were associated with grassland habitat last burned in 1993, two or three years previously. Microhabitat at Henslow's Sparrow use sites had lower tree density than random survey points, but neither shrub density nor military disturbance index differed between use sites and survey points during spring. In summer, the military track index was higher on Henslow's Sparrow's use sites. Habitat used by Henslow's Sparrows was consistently tall and dense vegetation with high litter cover during early spring, late spring, and summer whereas the vegetation of random survey points changed in response to vegetation growth. Characteristics of Henslow's Sparrow use sites included high cover by litter and dense, structurally homogeneous vegetation, whereas litter depth and standing dead vegetation, physiognomic diversity, and military disturbance did not differ from random survey points. *Received 10 May 1999, accepted 5 Sept. 1999.*

Many grassland birds of the Midwest and the Northeast have experienced severe population declines since 1950 (Robbins et al. 1986, Herkert 1994a). These declines coincide with significant reductions in grassland habitat throughout these regions (Smith 1981, Askins 1993, Samson and Knopf 1994). Henslow's Sparrow (*Ammodramus henslowii*) has declined throughout its range at a rate of 9.0% per year from 1966 to 1996 (Sauer et al. 1997) and thus has been included on the National Audubon Society's Blue List of declining species since 1974 (Arbib 1979; Tate 1981, 1986; Tate and Tate 1982). The species was identified as a migratory nongame species of management concern in 1987 (U.S. Fish and Wildlife Service 1987, 1995; Schneider and Pence 1992; Pruitt 1995), is designated as a Species in Need of Conservation in Kansas (Kansas Department of Wildlife and Parks 1986), and concern for the species continues.

Henslow's Sparrows are believed to require areas of tallgrass prairie that are at least 30 ha and that have not been recently disturbed by events such as fire (Zimmerman 1988, 1992; Herkert 1994b) or haying for one or more years (Herkert 1994b, Swengel 1996). Henslow's Sparrows require vegetation that is tall and dense, especially within 25–40 cm of the ground (Kahl et al. 1985, Zimmerman 1988). Zimmerman (1988) suggested that the presence of standing dead vegetation reduces live growth and provides open areas at ground level for foraging Henslow's Sparrows.

This study was developed with two major objectives: to determine the habitat selected by Henslow's Sparrows on Fort Riley at both the fine scale (the scale of habitat within individual territories) and the larger scale of plant community type, and to determine if a relationship exists between the intensity of military training disturbance to the vegetation and habitat selected by Henslow's Sparrows.

METHODS

Study area.—Fort Riley (39° 15′ N, 96° 50′ W), Kansas lies in the Flint Hills, which extend from Nebraska across Kansas and into Oklahoma. The Flint Hills are the largest remaining area of tallgrass prairie in the world (Reichman 1987) and occur near the western edge of Henslow's Sparrow range (Sauer et al. 1997). Most of the private land in the Flint Hills is used for cattle grazing. Grazing, hay harvest, and annual burning on Flint Hills pastures alter the tallgrass prairie by reducing litter and dense vegetation near the ground, which reduces habitat quality for Henslow's Sparrows (Zimmerman 1988). Fort Riley is a 40,273 ha permanent U.S. Army Forces Command installation and is the site of ongoing military training. Fort Riley is the largest expanse of public land in the Flint Hills and unlike private land, cattle grazing is excluded. There is mechanical disturbance in the form of mechanized artillery training and some hay cutting of native tallgrass species. Unlike the private rangelands in the

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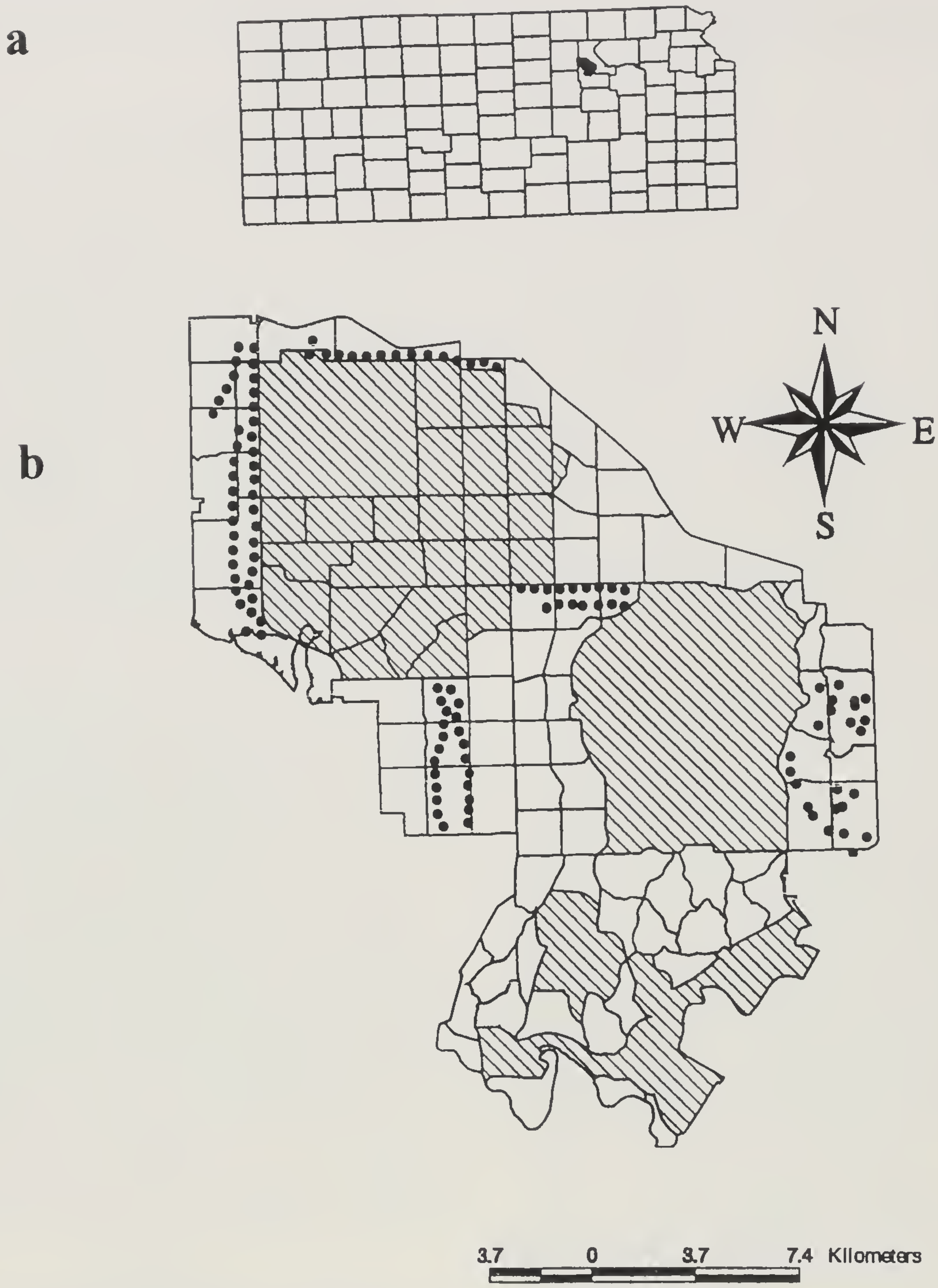

FIG 1. A. Location of Fort Riley Military Reservation, Kansas. B. Location of areas of restricted public access. Access is limited in the Multipurpose Range Complex, shaded area in northwest, and is never available in the impact zone, the shaded area in the center of the fort. The shaded areas in the south are cantonment areas. We placed the census points (circles) in tallgrass prairie habitat where access was most available (from Michaels and Cully 1998).

Flint Hills, most of which are burned annually. Fort Riley has a prescribed burn program that strives to burn at three year intervals. Thus, Fort Riley may have the largest tract of potential Henslow's Sparrow habitat in Kansas.

Bird surveys.—In 1995, 119 permanent bird survey points (survey points) were located in upland grassland habitats in areas of Ft. Riley with minimum access restrictions (Fig. 1) approximately 500 m apart along transects ranging from 5 to 7 km in length. Each survey point was marked with flagged fence posts (Fig. 1). Each transect was surveyed beginning at first light and was completed within three hours after sunrise. Surveys were not conducted during heavy fog, rain, or when wind speeds exceeded 20 km/hr. To minimize sampling bias, the order in which transects were surveyed each month and the starting point and direction in which points were sampled along the transect were varied randomly. A small number of survey points were excluded from analysis each year because military activity prevented access or the field was cut for hay prior to microhabitat measurements. From May to August, 1995 and from March to July, 1996 five-minute timed monthly surveys were conducted at each survey point using a modified variable circular plot method (Reynolds et al. 1980) to locate breeding Henslow's Sparrows. The Universal Transverse Mercator coordinates of the exact location of each Henslow's Sparrow seen or heard was recorded with a Global Positioning System unit as a Henslow's Sparrow use site. The date each bird was observed, the activity of the bird, and the type of perch being used (e.g., tree, shrub) when the bird was first located were recorded.

Birds were assumed to be defending a breeding territory at a site if a singing male was relocated at the same site on three or more subsequent morning visits (see Herkert 1994a). Birds making up loose breeding colonies (Wiens 1969) were determined to be independent breeding individuals based on territorial behavior, primarily simultaneous singing. The largest number of Henslow's Sparrows seen singing from a survey point on any of the monthly censuses during 1995 or 1996 was assumed to be the number of breeding pairs associated with that point that year. Thus, no bird was counted more than once during each year. Microhabitat data at Henslow's Sparrow use sites was only measured during 1996 so individual birds were only counted once for the microhabitat analyses. Separate analyses of macrohabitat association were made for the two years.

Large scale habitat.—An initial large scale habitat analysis of upland grasslands on Fort Riley was made using a tree-cover map developed by the Kansas Biological Survey (Lauver et al. 1996) and onsite visual estimates. Large scale habitats were defined for 250 m radius patches (19.6 ha) as grassland ($n = 35$) if plots contained fewer than 15 isolated shrubs (<4 m tall) or trees (>4 m tall) or no more than one copse less than 20 m in diameter. Savanna plots ($n = 44$) contained greater than 15 shrubs or trees but did not contain continuous, wooded riparian habitat. Woodland edge points ($n = 40$) were located within 100 m of extensive, wooded riparian habitat that ran through the plot. All of the survey points were placed in tallgrass prairie habitat. The landscape habitat category of specific Henslow's Sparrow use sites was determined with the same methods used for the survey points.

Permanent bird survey points and Henslow's Sparrow use sites were grouped into five burn treatments based on the year the site was last burned, and two hay treatments based on whether or not the site was cut for hay in 1995. A χ^2 test (SAS version 6.12 on a PC) was conducted to determine if the observed frequencies of Henslow's Sparrow use sites among the three habitat types, among the burn treatments, and among the hay treatments differed from the proportion of survey points in each treatment.

Fine scale vegetative structure.—Fine scale vegetation structure was sampled at Henslow's Sparrow use sites during the spring and summer of 1996 and at survey points during spring 1996 and summer 1995. One hectare sampling grids for survey points were permanently located randomly within 200 m of each survey point. One hectare vegetation sampling grids were also centered on Henslow's Sparrow use sites in order to describe Henslow's Sparrow fine scale habitat. The density of shrubs (<4 m in height) and trees (>4 m in height) was counted within the 1 ha sampling grid.

A point-intercept method was developed (Michaels and Cully 1998, modified from Rotenberry and Wiens 1980) to sample the structure of the herbaceous vegetation at each survey site and Henslow's Sparrow use site. Within the 1 ha sampling grid, 100 randomly located sampling points were selected. At each of the 100 points a 6 mm diameter rod marked at 10 cm intervals was dropped through the vegetation to record the vertical density of the vegetation as the number of contacts between the pole and vegetation in 10 cm intervals. At each sampling point, the number of contacts of vegetation within each decimeter of the sampling rod was recorded according to the physiognomic class (live grasses, live forbs, standing dead vegetation). These samples were used to calculate measures of herbaceous vegetative cover and vertical and horizontal vegetative structure. Total vegetative cover was estimated as the number of points with at least one of the physiognomic classes of vegetation. Percent cover by each physiognomic class present at a site was calculated from the frequency of occurrence of each class at all 100 sampling points. Physiognomic cover diversity (P) was calculated to show relative structural diversity of the vegetation using the reciprocal of Simpson's (1949) diversity index as

$$P = 1/\Sigma\, p_i^2,$$

where p_i is the proportional coverage of the i^{th} physiognomic class (Hill 1973, Wiens and Rotenberry 1981). This index can be understood to measure the effective number of physiognomic classes present in a sample, which could vary from one to three (live grass, live forb, and standing dead). Percent cover of litter was calculated as the number of points that contacted litter. When litter was present, its depth (cm) was measured and recorded. The maximum height of vegetation contacting the rod was also recorded. The vertical density of the vegetation was calculated as the mean number of contacts of vegetation with the rod. Two heterogeneity measures were calculated. The first is the coefficient of variation of the maximum height of the vegetation across the sampling plot. The second is the coefficient of variation of the vertical density of the vegetation across the sampling plot.

The severity of military disturbance to the vegetation was quantified at the fine scale. If disturbance was intercepted by the sampling rod, the sampling point was given a score indicating the intensity of disturbance: 1 (crushed vegetation, little soil disturbance), 2 (extensive disruption of the soil, little remaining vegetation), or 3 (permanent gravel road). A military disturbance index was calculated for each site as the sum of the disturbance scores for all 100 sampling points within the plot.

Principal components analysis.—The spring 1996 survey points encompassed the range of fine scale vegetative conditions available to grassland bird species at Fort Riley at the time when they were establishing

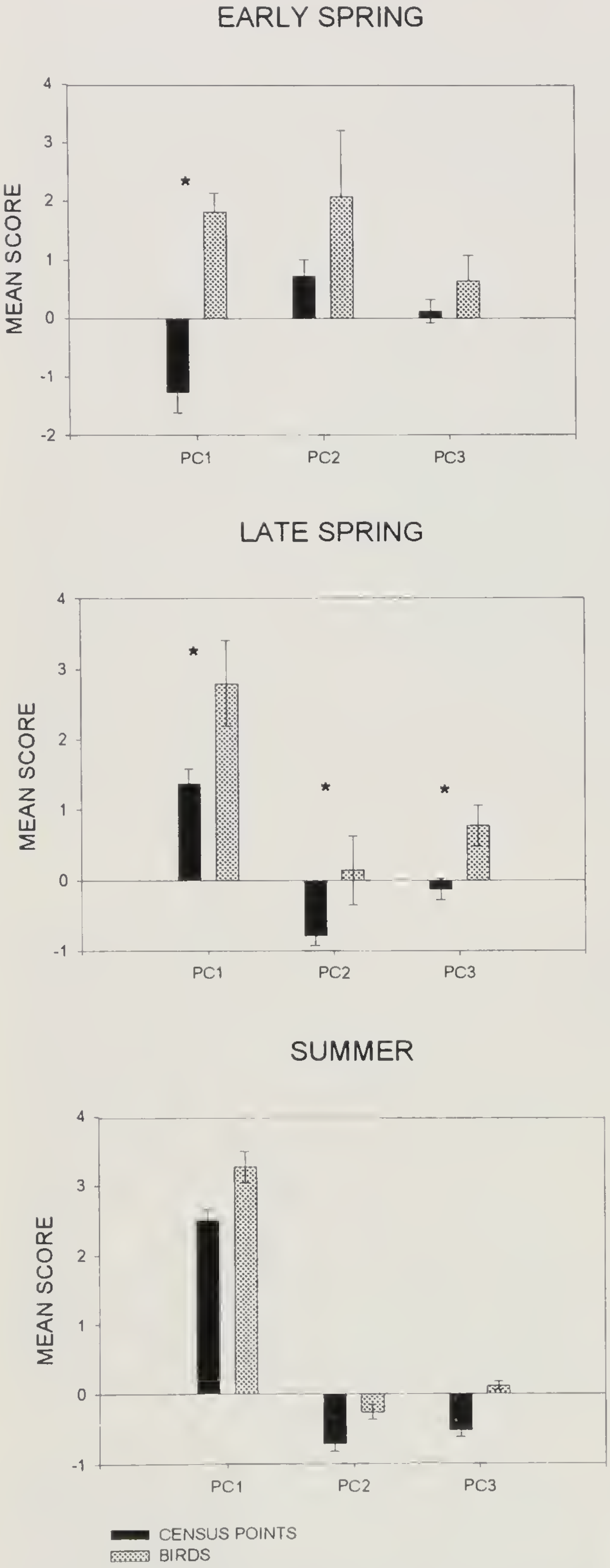

FIG. 2. Principal components scores of permanent bird survey points and Henslow's Sparrow bird centered points at Fort Riley Military Reservation, Kansas. See text for description of microhabitat variables associated with principal component axes.

territories (Zimmerman 1988). For this reason, these data were used as the baseline data for all comparisons. Because measures of vegetative structure are highly correlated with one another (James 1971, Wiens and Rotenberry 1981), a principal components analysis (PCA) was conducted (using SAS, Version 6.12 on a PC) on the spring data to identify the patterns of co-variation among the herbaceous vegetation variables. Principal components analysis has the advantage of reducing a large number of covarying variables to a smaller number of orthogonal components that maximize the variance accounted for in the data (Rotenberry and Wiens 1980, Gauch 1982). Habitat data from the Henslow's Sparrow use sites were also collected as at the survey points. The fine scale habitat data from Henslow's Sparrow use sites were then applied to the spring principal components to ordinate Henslow's Sparrow use sites in the principal component space defined by the survey points. By plotting Henslow's Sparrow use sites vegetation data in the principal component space defined by the spring survey point vegetation data, comparisons of the principal component scores using analysis of variance (ANOVA) could be made between use sites and survey points in order to detect non-random patterns of bird-habitat associations (Michaels and Cully 1998). Likewise, this method makes it possible to assess how the habitat at the survey points changed in PCA space as a result of plant growth as the seasons advanced. Spring vegetation was sampled with the intent of measuring the survey point vegetation in April, prior to the beginning of the growing season. However, because a reservation-wide training exercise announced in late April eliminated access to most of the study site during late April and early May, approximately half of the survey points were not sampled until after the beginning of the growing season in late May. The baseline principal components analysis, to which other samples were compared, was made up of the combined early and late spring fine-scale vegetation data. A series of ANOVAs conducted on the principal component scores for sites sampled before and after the closure showed significant changes in the three significant principal components. For this reason, the spring 1996 sampling period was treated as two separate sampling periods (early and late) and the principal component scores were grouped accordingly for further analysis. Early spring Henslow's Sparrow use sites included sites identified prior to 15 May, late spring from 16 May to 30 June, and summer, later than 30 June. All variables expressed as percentages were transformed using the arcsine square root transformation (Zar 1984) prior to analysis. Data are presented as mean ($\bar{x}$) ± standard error (SE). Significance was established at $P = 0.05$ for all comparisons.

The Shapiro-Wilk test (SAS Institute, Inc. 1992) was used to test the univariate assumption that the data were normally distributed and Levene's test (Milliken and Johnson 1984) was used to test the univariate assumption that the treatment group variances were equal. When the treatment variances were unequal, the SATTERTH option within the PROC MIXED procedure in SAS (SAS Institute, Inc. 1992) on a PC was employed to calculate appropriate degrees of freedom and fit the unequal variance model. If the Satterthwaite method did not change the results of the ANOVA, the test was assumed to be robust despite the heterogeneous variances and the original data were retained. If, by fitting the unequal variance model, the results of the ANOVA changed, the test was conducted using the new degrees of freedom.

RESULTS

Large scale.—During 1995, 36 singing male Henslow's Sparrows were located. Several of the singing males were found together, a pattern similar to the loose breeding colonies noted by Hyde (1939) and Wiens (1969). Most 1995 Henslow's Sparrow use sites (21 of 36) were located in grassland, 10 in savanna and 5 associated with woodland edge points ($\chi^2 = 10.8$; 2 df; $P = 0.005$). In separate 2×2 tests, grassland was selected more frequently than savanna ($\chi^2 = 4.9$; 1 df; $P < 0.03$), but savanna and woodland edge did not differ ($\chi^2 = 1.0$; 1 df; $P > 0.05$). In 1996, 21 Henslow's Sparrows were observed at survey points; 13 in grassland, 4 in savanna, and 4 in woodland ($X^2 = 8.4$; 2 df; $P < 0.02$). As in 1995, 2×2 tests showed grassland habitat significantly more frequently used than savanna or woodland edge ($\chi^2 = 5.8$; 1 df; $P < 0.02$), which were equal. Only 3 of 12 survey points that yielded Henslow's Sparrows in 1996 also had the species in 1995. In 1996, Henslow's Sparrows only used sites that were not hayed the year before. Approximately 30% of the study area was hayed in 1995 (33 of 104 sites); however, only 5 were at sites identified as grassland. The distribution among burn treatments of Henslow's Sparrow sites in 1995 was significantly different from that expected ($\chi^2 = 10.49$; 4 df; $P = 0.03$) with the majority (22 of 24) of Henslow's Sparrows selecting sites burned either two (15) or three (7) years previously (1993 and 1992). During 1996, at 21 Henslow's Sparrow use sites, 2 sites were burned two years earlier (1994); 18 sites were burned three years earlier (1993), and one site was burned four years earlier ($\chi^2 = 50.56$; 4 df; $P < 0.0001$). Thirty-three of 45 sites (73%) used by Henslow's Sparrows during 1995 and 1996 were burned in 1993.

Fine scale.—The PCA of the spring 1996 fine scale vegetation of the 13 microhabitat variables resulted in three principal components with eigenvalues greater than one. Together these accounted for 84% of the total variance present in the data (Table 1). Positive values of PC1 represent high total cover, vertical density, litter cover, and low vertical and horizontal heterogeneity. High positive values on PC1 are representative of undisturbed tallgrass prairie whereas large negative values represent vegetation that was disturbed either by fire or military activity. Positive values on PC2 represent high cover of standing dead vegetation, tall vegetation, high litter depth, and low cover of live grass and forbs, especially new growth close to the ground. Sites scoring highest on PC2 were those that had not been burned for three or more years, whereas those with negative values on PC2 were those burned earlier in 1996. Positive values on PC3 represent sites with high physiognomic diversity and relatively high indices of military disturbance.

Principal component scores for survey points on PC1 increased ($F = 78.4$; 2, 204 df; $P < 0.01$) from -1.3 in early spring ($n = 54$), to 1.4 in late spring ($n = 50$) and 2.5 ($n = 103$) by summer (Fig. 2). Values of survey points on PC2 were positive in early spring (0.73) and significantly different from late spring (-0.79) and summer (-0.72; $F = 23.2$; 2, 204 df, $P < 0.01$). Principal component scores on PC3 decreased from early spring (0.12) to summer (-0.52) and were intermediate in late spring (-0.13; $F = 6.06$; 2, 204 df; $P < 0.01$). Henslow's Sparrows use site scores did not differ among seasons on any PC axis, although there was a nearly significant difference ($F = 2.9$; 2, 18 df; $P = 0.08$) from early spring (2.09) to summer (-0.26) on PC2 (Fig. 2).

There was no significant difference in the density of shrubs between early and late spring combined Henslow's Sparrow use sites (10.08 ± 3.98, $n = 13$) and early spring survey points (10.76 ± 1.95; $F = 0.02$; 1, 66 df; $P > 0.05$). However, Henslow's Sparrow use sites had significantly lower tree densities (0.54 ± 2.68) than survey points (6.67 ± 1.32; $F = 4.21$; 1, 66 df; $P = 0.04$). The mean value of PC1 (vegetative cover and density, litter cover, or structural homogeneity) on Henslow's Sparrow use sites ($n = 7$) in early spring was significantly higher than survey points ($F = 10.07$; 1, 59 df; $P = 0.02$), whereas early

TABLE 1. Eigenvectors of fine scale vegetative variables for the first three principal components determined by a PCA of Spring 1996 bird survey site herbaceous vegetation data at Fort Riley, Kansas. Factor loadings $<|0.30|$ are omitted.

Variable	PC1	PC2	PC3
Eigenvalue	6.11	3.15	1.66
Variance explained	47%	24%	13%
Cumulative variance	47%	71%	84%
Cover in percent			
Total vegetation cover	0.393		
Litter cover	0.302		
Live grass cover		−0.358	
Live forb cover		−0.336	
Standing dead cover		0.374	
Physiognomic diversity			0.633
Vertical structure			
Litter depth		0.454	
Hits in first decimeter		−0.401	
Maximum height		0.330	
Vertical density	0.381		
Heterogeneity indices			
Coefficient of variation, vertical density	−0.379		
Coefficient of variation, maximum height	−0.359		
Military Disturbance			
Track index			0.588

spring Henslow's Sparrow use sites did not differ significantly from survey points on PC2 (F = 2.46; 1, 59 df; $P > 0.05$) or PC3 (F = 0.77; 1, 59 df; $P > 0.05$) (Fig. 2).

During late spring, Henslow's Sparrows (n = 6) used habitats that were significantly different from survey points on all three principal components, although differences on PC1 were less than they had been in early spring. By summer, survey point scores had converged on the summer Henslow's Sparrow use sites (n = 8) to the extent that there were no longer significant differences on any PC axis (Fig. 2). All Henslow's Sparrow use sites combined were greater than zero on PC1 and had a higher mean value on PC2 than combined early and late spring survey points (Fig. 3). No significant differences existed with regard to the military track disturbance index between Henslow's Sparrow use sites and survey points during early or late spring, but they did diverge in summer (Table 2).

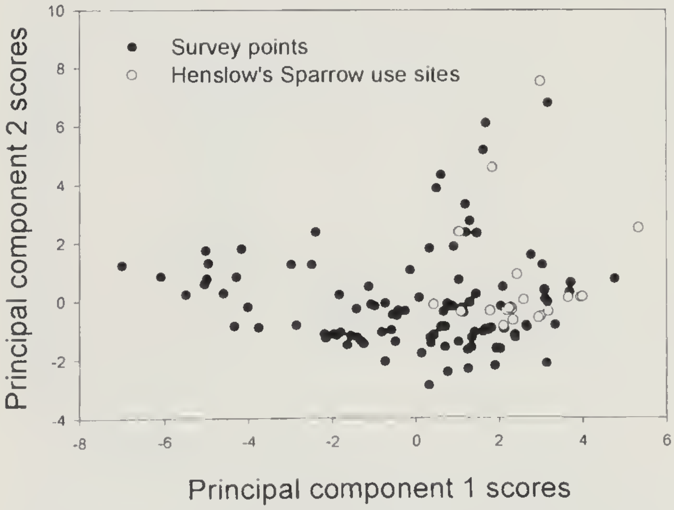

FIG. 3. Plot of Henslow's Sparrow use sites and survey points on principal components axes 1 and 2. Principal component 1 ordinates from undisturbed tallgrass prairie to highly disturbed prairie. Positive values on principal component 2 represent high cover of standing dead vegetation, tall vegetation, and deep litter.

DISCUSSION

Henslow's Sparrows used open grassland habitat with few trees at both the large scale of habitat type and at the fine scale. At the fine scale the density of shrubs for Henslow's Sparrow use sites did not differ from the survey points. Thus, the presence of some low woody vegetation did not reduce Henslow's

TABLE 2. Comparison of 1996 military track disturbance index between Henslow's Sparrow use sites and random survey points at Fort Riley Military installation, Kansas. The military track index measures the severity of military disturbance to the vegetation and has a potential range of 0 to 300.

Sampling period	Survey points	*n*	Henslow's Sparrow use sites	*n*	*P*
Early spring	59.2 ± 5.8	54	57.9 ± 11.9	7	>0.05
Late spring	49.4 ± 1.1	50	57.9 ± 8.0	6	>0.05
Summer	37.4 ± 2.5[a]	103	47.8 ± 3.4[a]	8	0.02[b]

[a] Unequal variance estimates.

[b] *P* value is the result of using unequal variance estimates. Difference of LS Means = −10.37, and SE of the difference = 4.19.

Sparrow use of the habitat at this scale. This is similar to observations of other authors who have also reported the presence of scattered bushes and shrubs in areas occupied by Henslow's Sparrows (Hyde 1939, Robins 1971, Bull 1974, Hanson 1994, Herkert 1994b).

None of the Henslow's Sparrows located on Fort Riley in 1996 were located in areas that had been hayed in 1995. Although 33 of 104 survey points were hayed in 1995, only 5 were in grassland sites, which were Henslow's Sparrows' preferred macrohabitat. Because the availability of hayed grassland sites in 1996 was low compared to the availability of non-hayed grassland, conclusions cannot be made from these data regarding the effects of haying on Henslow's Sparrow habitat selection at Fort Riley. Such conclusions will require long-term records regarding the frequency of harvest at survey and Henslow's Sparrow use sites. Because Henslow's Sparrows raise two to three broods per breeding season and nest as late as August (Robins 1971), hay cutting has the potential to directly affect the productivity of this ground nesting species (Smith and Smith 1992).

Most (96%) Henslow's Sparrow use sites at Fort Riley were located in sites last burned two or three years previously, a pattern of selection similar to that found in other studies (Herkert 1994b, Swengel 1996). During this study, 1993 burn sites were unique among other burned sites in that they reached the highest total vegetative cover and density (PC1) in late spring, rather than in summer, the pattern for 1994 and 1992 burned sites. This high cover and density early in the breeding season may have been important to Henslow's Sparrows establishing territories in April and May.

We found no differences in the severity of military disturbance to the vegetation between survey points and Henslow's Sparrow use sites during spring; however, track disturbance was higher on Henslow's Sparrow use sites in summer. We attribute this to the flatter terrain in areas frequented by Henslow's Sparrows being more attractive to military operations. To conclude that military disturbance to the vegetation does not adversely affect site selection by Henslow's Sparrows is not yet warranted. Military disturbance to the vegetation can indirectly influence avian site selection by altering vegetative structure. For example, the pattern of military disturbance can affect vegetative structure by crushing and fragmenting patches of herbaceous vegetation and reducing the effectiveness of fire in localized areas. Furthermore, there is evidence that vehicular disturbance changes both the structure and composition of grassland vegetation by reducing cover by vegetation and litter and increasing cover by annual grasses and forbs (Johnson 1982, Wilson 1988, Shaw and Diersing 1990). Although these changes may be apparent in the vegetation within a season or two, they may take longer to affect bird habitat selection. We also noted that the bird territories were established before disturbance was measured. The direct and indirect effects of track disturbance on productivity are unknown and warrant further investigation.

The principal components analysis of vegetation at the survey points in early spring, late spring, and summer illustrates the habitat changes that occurred with plant growth through the growing season in tallgrass prairie habitats at Fort Riley. The mean scores of the survey points on PC1 increased through the season, reflecting the increasing importance of live grasses and forbs, and increasingly homogeneous vegetation as the seasons progressed. Principal component 2 scores declined as the seasons progressed, indicating decreasing prevalence of standing dead vegetation and a shift in importance from dead to live vegetation close to the ground. Permanent bird survey points score also declined on PC3 from early spring through summer, which indicated reduced physiognomic diversity and a lower incidence of vehicle tracks at survey points.

Henslow's Sparrow use sites did not differ significantly between sampling periods with respect to the measured vegetative variables despite concurrent changes in these variables through time for the survey points. This consistent pattern for the Henslow's Sparrow use sites suggests the importance of these vegetative variables to Henslow's Sparrow habitat selection. Vegetative characteristics consistently associated with Henslow's Sparrow use sites included high cover by litter and by dense, structurally homogeneous vegetation (high values of PC1). Mean values of PC2 (litter depth, and height and cover by standing dead vegetation) and PC3 (physiognomic cover diversity and disturbance index) did not differ between use sites and survey points during early spring. However, as mean values of PC2 and PC3 decreased across survey points during late spring, the difference between Henslow's Sparrow use sites and survey points became significant. Relative to survey points, Henslow's Sparrow use sites retained higher cover by standing dead vegetation and deeper litter (high values of PC2) in late spring. Those differences disappeared by summer. Scores on PC3 did not differ between Henslow's Sparrow sites and survey points during early spring; however, in late spring Henslow's Sparrow use sites and survey points were different. The differences identified in PC3, physiognomic diversity and track index, may be a result of sampling error. These results show, as Wiens (1989) noted, that the timing of studies investigating bird-habitat associations may greatly influence the detection of significant patterns of habitat selection.

At this time, management practices at Ft. Riley provide some habitat for Henslow's Sparrows. The desired practice of three year intervals for burns is appropriate; however, frequent wildfires reduce the amount of area suitable for Henslow's Sparrows. There are no records of which areas are hayed each year, but all areas where we recorded Henslow's Sparrows are open to haying. Henslow's Sparrow habitat could probably be increased on Fort Riley by establishing a program to rotate areas available for haying among years to complement the fire rotation program. Ft. Riley currently provides important habitat for Henslow's Sparrows and other species and we encourage the Natural Resources staff to continue their good work.

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MIGRANT STOPOVER AND POSTFLEDGING DISPERSAL AT A MONTANE FOREST SITE IN VERMONT

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ABSTRACT.—To investigate the use of high elevation fir forests by fall passage migrants, we conducted standardized mist-netting and banding at a 1150–1175 m elevation site on Mt. Mansfield in north-central Vermont during the autumns of 1995–1997. Overall, we captured 3024 individuals of 62 species in 10,048 cumulative net hours (30.1 birds/100 net hr). We divided species into 3 classes: (1) those breeding regularly on Mt. Mansfield above 916 m elevation (16 species), (2) those breeding only sporadically or at very low densities above 916 m (6 species), and (3) those occurring only as transients (40 species). Breeding species accounted for 68% of new captures, followed by transients (22%), and sporadic/low density breeders (10%). Of the ten most abundant species captured, only two, Black-throated Blue Warbler *(Dendroica caerulescens)* and Ovenbird *(Seiurus aurocapillus)*, were transients, accounting for 50% and 9%, respectively, of all transient captures. Hatching-year birds accounted for 94% of known-age transients and 81% of known-age individuals among locally breeding species. Recapture rates of transients were extremely low (0.3%), while recapture rates among species known to breed locally (including presumed transient individuals) were higher (2.2%). Nearly 75% of all birds captured were very lean at first capture, and only 26% of recaptured individuals increased their fat scores between first and final captures. Weight changes of recaptured birds varied: 48% lost weight, 44% gained weight, and 8% maintained the same weight between first and final captures. Our data suggest that conditions on the Mt. Mansfield ridgeline are not conducive to prolonged migratory stopovers and that most migrants may be unable to meet their energetic requirements for continued migration. However, we believe that montane forest habitats may be preferentially selected by those migrants that use them for breeding. We further believe that montane fir forests may be an important postfledging dispersal habitat for Black-throated Blue Warblers and other low or mid-elevation breeding species, and that conservation planning for montane forest sites should carefully consider the needs of migrants outside the breeding season. *Received 18 March 1999, accepted 25 Oct. 1999.*

Of the numerous demands that migrant birds face during their annual migrations, selection of enroute stopover habitat is paramount. Choice of stopover habitat may play a pivotal role in determining a migrant's survival and is dependent both on intrinsic suitability of the habitat and on extrinsic factors such as weather, time constraints, energetic condition, and availability of the habitat (Hutto 1985, Moore and Simons 1992). Stopover migrants must resolve potentially conflicting needs to meet their energy demands, avoid predation, adjust to unfamiliar habitats, compete with other migrants and residents, and deal with unfavorable weather conditions (Moore et al. 1995). Loss or degradation of stopover habitat may have significant adverse effects on migrant populations (Moore et al. 1995, Yong et al. 1998).

Despite recent heightened interest in stopover ecology and its conservation implications (see Moore and Simons 1992, Moore et al. 1995, Hutto 1999), few researchers have focused on high elevation forested habitats of North America (but see Hall 1981, Hall and Bell 1981). In the northeastern United States, montane forests occupy a prominent, although geographically limited, space in the regional landscape. Their maximum extent is only 0.39% of all land area (uncorrected for topography) above 915 m elevation in northern New England and New York, and they occur as habitat "islands" of varying size and distance from one another (see Atwood et al. 1996). These forests support a distinctive assemblage of breeding bird species, including most of the world's population of Bicknell's Thrush (*Catharus bicknelli*; Rosenberg and Wells 1995; Rimmer and McFarland, unpubl. data). High elevation forests in the Northeast are potentially threatened by an array of factors including atmospheric pollution, global warming, ski resort development, telecommunications facilities, and wind power development (Weiss and Millers 1988, Atwood et al. 1996, Rimmer 1996). Although the significance of these habitats for breeding birds has become increasingly well-recognized, virtually nothing is known about the importance of

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montane forests as stopover habitats. Similarly, the use of montane forests during the postfledging period, when availability and quality of suitable habitats are especially critical (Anders et al. 1998), has been poorly studied.

During the course of field research on Bicknell's Thrush in September of 1994, we observed marked influxes of passage migrants on three widely separated Northeast peaks (Mt. Mansfield in north-central Vermont, Equinox Mountain in southwest Vermont, and Slide Mountain in the Catskills of New York). These concentrations included many species that breed only in lower elevation habitats, leading us to consider that montane forests might provide important fall stopover habitats. In this paper we present the results of a three-year study on Mt. Mansfield to examine the extent and patterns of migrant stopover use at a single montane forest site.

STUDY AREA AND METHODS

We conducted standardized mist-netting and banding at a 1150–1175 m elevation site on the ridgeline of Mt. Mansfield (44° 32′ N, 72° 49′ W) in north-central Vermont during the autumns of 1995–1997. Mt. Mansfield, Vermont's highest (1339 m elevation) and second largest (769 ha area above 915 m elevation) mountain, is characterized by a north–south ridgeline that extends about 4 km southward from the summit. Forming part of the spine of Vermont's Green Mountains, Mt. Mansfield is isolated from similar montane forest patches to the northeast (5.1 km) and south (9.9 km). The ridgeline forest is dominated by balsam fir *(Abies balsamea),* with lesser amounts of red spruce *(Picea rubra),* heart-leafed paper birch *(Betula papyrifera* var. *cordifolia)* and mountain ash *(Sorbus americana).* This vegetation is stunted by chronic exposure to high winds and heavy winter ice loads, and is extremely dense. Canopy heights average 1–4 m (mean 2.2 m) and stem densities average 8274/ha (McFarland and Rimmer, unpubl. data). Weather can be severe at any time of year, and snow and ice storms are frequent after mid-September. Mean minimum temperatures on the Mt. Mansfield ridgeline during the months of August through October in 1995–1997 were 3.3° C colder than those at a northern hardwoods forest site in nearby Underhill at 400 m elevation (10.1° C vs 12.8° C in August, 5.5° C vs 8.0° C in September, 0° C vs 4.6° C in October, respectively; Vermont Forest Ecosystem Monitoring, unpubl. data). Total precipitation during the same period was 74 cm higher on Mt. Mansfield than at Underhill (185 cm vs 111 cm, respectively). The ridgeline is moderately impacted by human activities, with narrow gravel roads, hiking trails, a 0.25 ha parking lot, several telecommunications towers, small buildings, and occasionally heavy foot and vehicle traffic during the summer and fall.

We operated 10–20 mist nets (12 m × 2.6 m, 36-mm mesh) over a study area of about 8 ha from 2 August–13 October in 1995, 1 August–10 October in 1996, and 5 August–10 October in 1997. Netting was terminated in mid-October of each year because of deteriorating weather and closure of the mountain toll road. Because of extremely dense habitat and the ridgeline's protected status as a University of Vermont Natural Area, net sites were restricted to existing hiking trails and natural openings. Thus, we were unable to space nets in a regular pattern over the study area. Nets were opened for 6 hr/d for 5 d/wk beginning at dawn, except in conditions of rain, ice, snow, or high winds. Sampling effort (hours of operation/12 m mist-net) was recorded daily. Although numbers of nets varied among years, net sites remained constant. All captured birds were banded with a U.S. Fish and Wildlife Service aluminum leg band, aged and sexed, and the following data were recorded: (1) body weight to the nearest 0.1 g, (2) subcutaneous fat class, (3) unflattened wing length, (4) degree of skull pneumatization (Pyle 1997), (5) extent of flight feather or body molt, (6) time of banding, and (7) capture site. We used the fat classification system described by Cherry (1982): 0 = no visible subcutaneous fat; 0.5 = traces of visible subcutaneous fat; 1 = solid sheet of fat lining the furculum, but concave; 2 = fat filling the furculum, but not mounded; 3 = fat filling furculum, and bulging out but not meeting layer of fat from abdomen; and 4 = furcular and abdominal fat mounded and meeting. For birds recaptured within a single morning, only body weight and fat class were recorded on subsequent captures. Weights were not corrected for time of day because we found no significant correlation between initial capture weights and time of day for any of the ten most commonly captured species (see methods in Winker et al. 1992; range of r^2 values = 0.0003–0.0439).

Because our netting sampled many locally breeding species and was initiated during late stages of nesting and postfledging parental care in each year, we assigned all species in our total sample of captures into one of 3 classes. These included: (1) species regularly breeding on Mt. Mansfield above 915 m elevation (breeders), (2) species breeding sporadically or at low densities above 915 m elevation (sporadic breeders), and (3) species known to occur only as transients above 915 elevation (transients). While many individuals in the two breeding classes, especially those captured in September and October, were most likely transients from other breeding areas, we were unable to unambiguously distinguish these individuals from local breeders. This classification, while arbitrary, enabled us to examine stopover differences between known transient species and those species adapted to montane spruce-fir forests for breeding.

We compared stopover patterns of Black-throated Blue Warblers (*Dendroica caerulescens*), our most commonly captured transient species on Mt. Mansfield, with those from another high elevation migration banding site, Allegheny Front Migration Observatory

TABLE 1. Mist-netting effort and capture rates on Mt. Mansfield, Vermont.

Year	# Net hrs	# Days	# New captures	Birds/100 net hrs.	# Species
1995	3115	45	939	30.2	52
1996	4157	46	1442	34.7	46
1997	2776	37	643	23.2	44
Total	10.048	128	3024	30.1	62

(Allegheny Front), at about 1200 m elevation in northern West Virginia (39° 02′ N, 79° 18′ W). The physical characteristics and banding operations at this site, approximately 820 km southwest of Mt. Mansfield, are described by Hall and Bell (1981). We compared only those capture data collected in August–October 1995–1997 at each site. We also conducted a more limited comparison of our Black-throated Blue Warbler data with those for the same period at two other long-term, inland banding stations at low elevations, the Vermont Institute of Natural Science (VINS) in Woodstock, Vermont (43° 36′ N, 72° 32′ W, 106 km south of Mt. Mansfield) and the Powdermill Nature Reserve (Powdermill) in Rector, Pennsylvania (40° 10′ N, 79° 16′ W, approximately 725 km southwest of Mt. Mansfield and about 130 km north of Allegheny Front). The Vermont Institute of Natural Science is characterized by second-growth shrub-scrub habitat embedded in a landscape matrix of northern hardwoods forest (Rimmer, Faccio, and McFarland, unpubl. data), while the Powdermill site is composed of old fields and second-growth deciduous forest in various seral stages, with several small ponds and wetlands (Leberman 1976).

RESULTS

Both sampling effort and capture rates varied considerably among the three years of netting on Mt. Mansfield (Table 1). Differences in sampling effort among years resulted from the operation of fewer nets in 1995 (10 in August, 15 in September and October) than in 1996 and 1997 (15–20 in each year), and unusually inclement weather in 1997 that often caused us to close the nets. Relatively low capture rates in 1997 may have resulted in part from frequent and prolonged inclement weather conditions, especially during the peak migration period in September.

Of the 62 species we captured on Mt. Mansfield, 22 (35.5%) locally breeding species accounted for 78% of all captures and 40 transient species accounted for 22% of the total individuals captured. Of these 40 transient species, 33 (82.5%) were Nearctic-Neotropical migrants (see Rappole et al. 1983). Of species in the two breeding classes, only 8 (36.4%) are considered Nearctic-Neotropical migrants. Numbers of transients peaked in late August to mid-September, while captures of individuals in the two breeding categories peaked later, in mid-September to early October (Appendix).

The ten most abundant species captured accounted for a large proportion (82.8%) of the total number of individuals captured (Appendix). Five of these [Yellow-rumped Warbler (*Dendroica coronota*), Blackpoll Warbler (*Dendroica striata*), Dark-eyed Junco (*Junco hyemalis*), White-throated Sparrow (*Zonotrichia albicollis*), and Bicknell's Thrush] are among the most common breeding species on the Mt. Mansfield ridgeline (Rimmer and McFarland, unpubl. data). Captures of Yellow-rumped and Blackpoll warblers, in particular, greatly exceeded their overall relative breeding abundance, suggesting that many transients augmented local populations of these two species in fall. Ruby-crowned and Golden-crowned kinglets *(Regulus calendula* and *R. satrapa)* are uncommon breeders on the ridgeline, and nearly all individuals we captured were undoubtedly transients. Of the ten most abundant species, only two [Black-throated Blue Warbler and Ovenbird (*Seiurus aurocapillus*)] were true transients, accounting for a disproportionate number (50.2% and 9.2%, respectively) of all transient captures. Of the 19 transient species represented by 5 or more new captures (Appendix), 14 (73.7%) are characteristic breeders of mature northern hardwoods and mixed forests that generally occur below elevations of 760 m on Mt. Mansfield and throughout northern New England (DeGraaf et al. 1992).

Age ratios.—Hatching-year (HY) birds accounted for 94% of known-age transient captures, 82% of individuals of regularly-breeding species, and 75% of sporadic breeders (Appendix). Age ratios varied markedly among species. Among the 20 species with at least 20 new captures, 5 had HY ratios of 97–100%; of these, only Golden-crowned Kinglet breeds above 915 m elevation on Mt. Mansfield. Eight of the 20 most abundant species had HY ratios less than 75%; all breed at the site. With the exception of Bicknell's Thrush, we suspect that the majority of individuals of these species were transients.

Recapture rates.—Overall, we recaptured very few birds on the Mt. Mansfield ridgeline one day or more after initial capture (Appendix). Recapture rates of transients were extremely low (0.3%), while recapture rates among species known to breed locally (including presumed transient individuals) were higher (2.7%). Bicknell's Thrush, which appears to remain on or close to its breeding and possibly natal territories until southward departure in late September (Rimmer and McFarland, unpubl. data), had the highest recapture rate (15.1%). Second was the Black-capped Chickadee (*Poecile atricapillus* 12.2%), which may be one of very few species to regularly occur in winter above 915 m elevation on Mt. Mansfield (Rimmer and McFarland, pers. obs.). There were no significant differences in the recapture rates of after hatching-year (AHY) individuals (2.6%) and HY birds (1.7%; $\chi^2 = 2.29$, df = 1, $P > 0.05$).

Fat loads and weight changes.—Nearly three quarters (72.7%) of all birds captured on Mt. Mansfield were lean (fat class 0 or 0.5) at first capture. Individuals of transient species carried lower initial fat stores than those of species in the two breeding classes combined (85.8% and 69.4% of scores, respectively, in fat classes 0 or 0.5; $\chi^2 = 69.8$, df = 1, $P < 0.001$). Few birds carried visibly large fat loads (fat class 2 or 3) upon initial capture or subsequent recapture. Significantly fewer (1.1%) individuals among strictly transient species had initial fat scores of 2 or 3 than birds in the two breeding classes combined (8.9%; $\chi^2 = 38.6$, df = 1, $P < 0.001$). Overall, HY birds were leaner than AHY individuals (78.7% and 57.4%, respectively, of initial fat scores in classes 0 or 0.5; $\chi^2 = 94.9$, df = 1, $P < 0.01$). This difference was more pronounced among transient species (87.5% HYs and 64.3% AHYs with initial fat scores of 0 or 0.5) than among birds in the two breeding classes (75.7% HY and 56.7% AHY with initial fat scores of 0 or 0.5; $\chi^2 = 34.1$, df = 1, $P < 0.001$).

A comparison of fat scores among the two most common breeding species, Myrtle and Blackpoll warbler, and the two most commonly captured transient species, Black-throated Blue Warbler and Ovenbird, further highlights the differences between these two classes of migrants on Mt. Mansfield. Among Blackpoll Warblers, 24.5% of all birds captured (20.3% of HYs, 35.3% of AHYs) had initial fat scores of at least 1; 2.9% of birds had fat classes of 2 or 3. Among Myrtle Warblers, 16.7% of all captures (13.3% of HYs, 45.0% of AHYs) were of birds with fat classes of at least 1; 1.9% of individuals had fat scores of 2, none were captured with a fat class of 3. Among Black-throated Blue Warblers, only 7.6% of all birds captured (7.5% of HYs, 10.0% of AHYs) had fat scores of at least 1 and none was captured with scores of 2 or 3. Among Ovenbirds, only 6.7% of all captures (6.8% of HYs, 0% of AHYs) were of birds with fat classes of at least 1; 1 individual had a fat score of 2.

Our sample of recaptured individuals was too small to statistically analyze fat or weight changes of individuals within or among species. However, of the 52 recaptured birds that provided weight change data (uncorrected for body size, time of day, or length of stay), 25 (48.1%) lost weight, 23 (44.2%) gained weight, and 4 (7.7%) maintained the same weight between first and final captures. Of the 53 recaptures for which we recorded both initial and final fat scores, 30 (56.6%) maintained the same class, 14 (26.4%) increased by at least one class, and 9 (17.0%) decreased by at least one class. Few dramatic changes in weights or fat classes were recorded. Twenty-eight (58.3%) of the individuals that experienced weight changes gained or lost less than 5% of their original weight, while 15 (56.3%) birds experienced changes from 5–10%. Only 3 (6.3%) birds gained or lost more than 15% of their original weight. Among transient species, the only individual that provided weight and fat change data was a Lincoln's Sparrow (*Melospiza lincolnii*) that gained 2.5 grams (16.1% of original weight) and increased its fat class from 1 to 3 between 6 and 21 September 1995.

Black-throated Blue Warbler.—A striking feature of our results was the predominance of Black-throated Blue Warblers in our sample, accounting for more than half of all transients captured. We captured nearly five times as many Black-throated Blue Warblers as Ovenbirds, the second most abundant transient species (Appendix). Comparison of Mansfield and Allegheny Front data show similarly high capture rates (birds/100 net hr), while Black-throated Blue Warbler capture rates at the two

TABLE 2. Summary of Black-throated Blue Warbler (BTBW) fall capture data (1995–1997) at Mt. Mansfield. Allegheny Front Migration Observatory (AFMO), Vermont Institute of Natural Science (VINS), and Powdermill Nature Reserve (PNR).

Banding site	# New BTBW captures	BTBW /100 net hrs	% BTBW in total banded sample	% Recaptured	% HY[b]
Mansfield	338	3.4	11.2	0	97.0
AFMO	1479	7.4	16.4	0.2[a]	78.8
VINS	19	0.1	0.5	5.3	73.7
PNR	140	0.3	0.6	2.9	92.1

[a] AFMO recapture data from 1997 only.
[b] Hatching-year birds.

low elevation sites, VINS and Powdermill, were much lower (Table 2). Of the total banded sample at each site in 1995–1997, Black-throated Blue Warblers accounted for a significantly higher proportion of all new captures at Mt. Mansfield and at Allegheny Front than at VINS and Powdermill (Table 2; χ^2 = 3584, df = 3, $P < 0.001$).

Recapture rates showed a reversed pattern of variation among the 4 sites (Table 2). Although recapture data were not systematically collected at Allegheny Front, the numbers of Black-throated Blue Warblers recaptured at that site are negligible (Hall, unpubl. data). In 1997, the only season for which such data were available, only 1 of 603 (0.2%) banded Black-throated Blue Warblers at Allegheny Front was recaptured. No individual of this species was ever recaptured on Mt. Mansfield. At the two lowland sites, recapture rates were markedly higher than at the two montane forest sites (Table 2). Although recapture samples were insufficient to enable statistical comparisons of stopover lengths, fat gains, or weight changes among sites, the one individual recaptured at VINS, a HY female, remained on site a minimum of 4 d and gained 2.9 g. Three Powdermill birds, all HY, had mean minimum stopover lengths of 2.3 d (range = 1–4 d) and mean weight gains of 0.2 g (range = −0.2–0.5 g).

Mt. Mansfield differed from the 3 other sites in having a significantly higher ratio of HY/AHY Black-throated Blue Warblers (Table 2; difference between Mansfield and Powdermill: χ^2 = 5.52, df = 1, $P = 0.02$). Ratios of HY/AHY birds at Allegheny Front and VINS did not differ significantly from one another (χ^2 = 0.29, df = 1, P > 0.05; Table 2). The preponderance of HY birds at Mt. Mansfield was not reflected at the southern high elevation site (Allegheny Front), although HY sex ratios were nearly 1:1 at both sites (167 males, 154 females at Mt. Mansfield; 582 males, 592 females at Allegheny Front). At both Mt. Mansfield and Allegheny Front, HY birds preceded AHY individuals, but there was a less discernable peak of movement overall at the northern site than at Allegheny Front (Fig. 1). At Mt. Mansfield, Black-throated Blue Warblers were captured at a more or less steady rate from early August through September, with some birds occurring into October; however, 55.6% of all captures were in August. At Allegheny Front, numbers of this species were relatively low through August (7.5% of total captures), then rapidly increased to a peak in mid-September and decreased into October, with few birds appearing after 10 October (Fig. 1). At both sites, HY birds occurred throughout the species' overall range of capture dates, but a much more pronounced HY peak was evident at Allegheny Front than at Mt. Mansfield. At VINS, 106 km south of Mansfield, only 1 Black-throated Blue Warbler was captured before 5 September and only 3 after 1 October; the remaining 15 birds (78.9%) were captured between 6–24 September. At Powdermill, only 10 individuals (7.1%) of this species were captured in August, 109 (77.8%) in September, and 21 (15%) in October.

DISCUSSION

Few migration stopover data from other montane forest sites in North America or elsewhere are available for comparison to our results on Mt. Mansfield. These suggest that the Mt. Mansfield ridgeline does not generally support large numbers of stopover migrants in fall. The 3-yr mean of 30.1 new captures/100 net hr is lower than that of other regional fall migration banding operations at inland sites during the same period, including southern sites like Allegheny Front (40.0 birds/100 net hr; Hall, pers. comm.) and Powdermill (44.8 birds/100 net hrs; Mulvihill and Leberman, pers. comm.), and well below that of more northern sites like Braddock Bay Bird Observatory (71.3 birds/100 net hr; Brooks 1996,

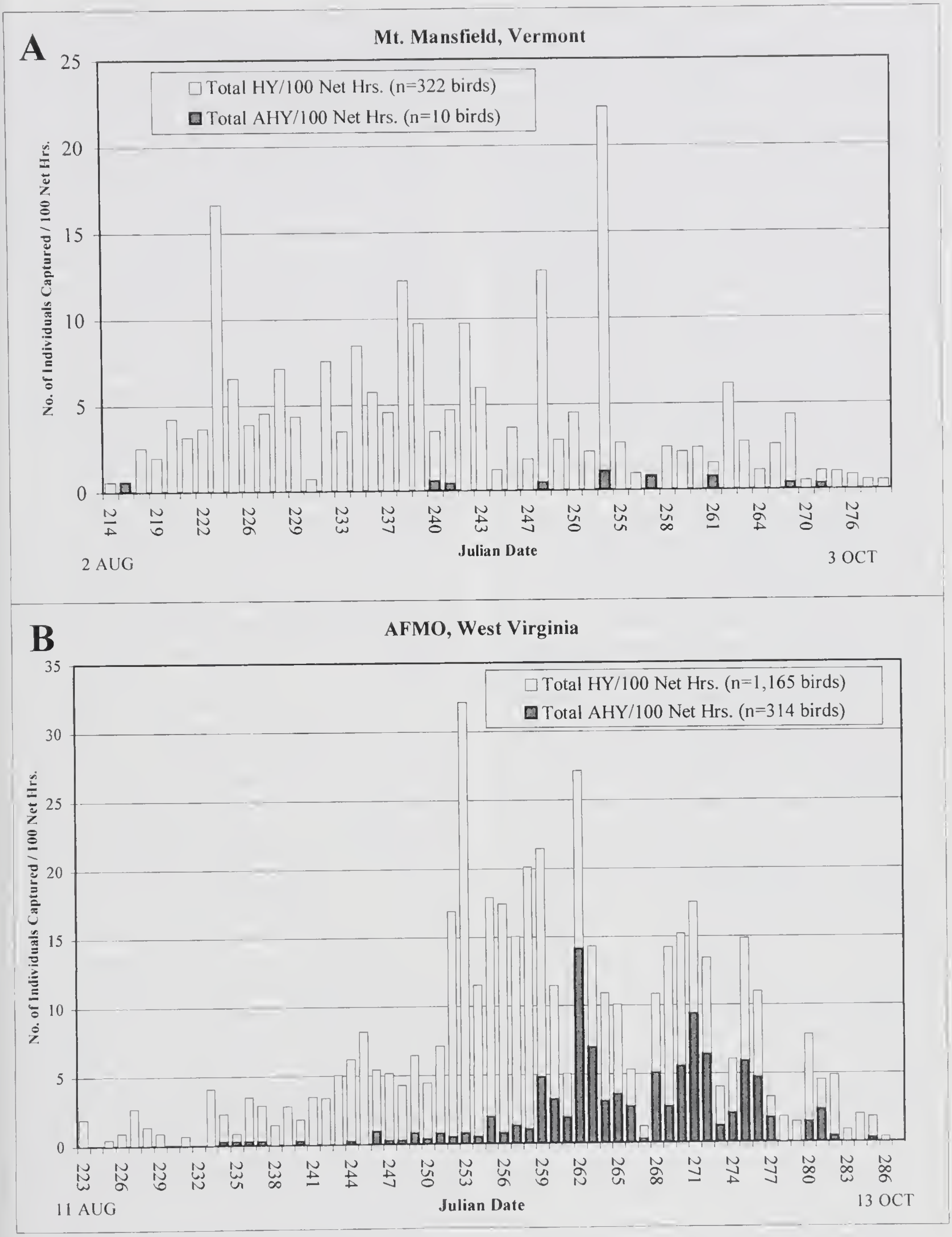

FIG. 1. Distribution by date of Black-throated Blue Warbler new captures at (A) Mt. Mansfield and (B) Allegheny Front Migration Observatory (AFMO), 1995–1997. Totals represented as birds/100 net hours.

1997, 1998) and Kestrel Haven Farm Avian Migration Observatory (120.0 birds/100 net hr; Gregoire 1997, 1998), both in central New York. Within Vermont, however, stopover volume, as measured by new captures, was higher at Mt. Mansfield in 1995–1997 than at VINS (20.8 birds/100 net hr; Rimmer, Faccio, and McFarland, unpubl. data). This suggests that Mt. Mansfield's prominent ridgeline may concentrate transients more than a lowland site like VINS, which has few physiographic features that act as a stopover focus for migrants. However, several local factors such as vegetation and weather vary between these two (and other) sites and may affect the relative capture probabilities of migrants, limiting the usefulness of between- or among-site comparisons of relative abundance (see Remson and Good 1996).

Eight of the ten most abundant species captured on Mt. Mansfield were regular or sporadic breeders (Appendix) and accounted for 70% of all captures. While some of these had undoubtedly nested or fledged locally, we believe that our samples were composed largely of transient individuals. Myrtle and Blackpoll warblers alone accounted for 24.9% and 13.7%, respectively, of our total banded sample, greatly exceeding their relative abundance as breeders on Mt. Mansfield (Rimmer and McFarland, unpubl. data). Their numbers peaked in early October and mid-September, respectively, well after each species' main period of fledgling independence on Mt. Mansfield (Rimmer and McFarland, unpubl. data), further suggesting that transients greatly augmented numbers of local breeders and HY birds. At VINS, the two species comprised only 2.8% and 0.2%, respectively, of the 1995–1997 fall totals (Rimmer, Faccio and McFarland, unpubl. data). The predominance of presumed transients of species that breed on Mt. Mansfield's ridgeline, and their relative scarcity at the low elevation VINS site only 100 km south, suggests that montane forest habitats may be preferentially selected by those migrants adapted to use them for breeding.

Conversely, Mt. Mansfield may be avoided by some transient species that do not inhabit montane forests. Although we have no direct evidence for this, certain groups of common transient genera and species at the VINS site were nearly or completely absent from our capture samples, including all flycatchers (Least Flycatcher, *Empidonax minimus; n* = 1), Veery *(Catharus fuscescens*; *n* = 6*)*, Wood Thrush (*Hylocichla mustelina*; *n* = 1), all mimid species (Brown Thrasher, *Toxostoma rufum*; *n* = 1), most shrub-scrub species, and all grassland species. Further indirect evidence of stopover bypass was obtained through automated recordings of nocturnal flights over Mt. Mansfield during 1997 and subsequent spectrographic analysis of nocturnal flight calls (Evans 1994, pers. comm.). Several species rarely or never documented on the ground or in mist nets were identified migrating overhead. Among those landbird species whose nocturnal flight calls were identified on 10 nights between 29 August and 26 September were Black-billed Cuckoo *(Coccyzus erythropthalmus*; *n* = 2), Veery (*n* = 42), Savannah Sparrow *(Passerculus sandwichensis*; *n* = 1*)*, and Bobolink *(Dolichonyx oryzivorus*; *n* = 6; Evans, pers. comm.). Thus we suspect that some transients regularly overfly Mt. Mansfield, possibly to avoid stopping in its unfamiliar or seemingly unsuitable habitats.

Among strictly transient species captured on the Mt. Mansfield ridgeline, most (74%) breed in mesic northern hardwoods and mixed forests that occur on Mt. Mansfield's lower slopes and at elevations below 760 m throughout northern New England. Few species restricted as breeders to Canada's and northern New England's extensive lowland boreal forest biome were represented in our samples, and these were captured in very small numbers. Among transient species with 5 or more new captures (Appendix), only Tennessee Warbler *(Vermivora peregrina)*, Bay-breasted Warbler *(Dendroica castanea)*, and Lincoln's Sparrow are true boreal habitat specialists. The disproportionate abundance of northern hardwoods breeding species on Mt. Mansfield suggests the possibility of an upslope post-breeding or postnatal dispersal rather than or in addition to migration stopover among these species. The strong elevational zonation on Mt. Mansfield is such that only about 1.5 km of distance separates the ridgeline fir-spruce forest from the lower northern hardwoods slopes.

Age-related stopover differences.—The predominance of HY individuals (94% overall) among transient species on Mt. Mansfield is contrary to the findings reported from most inland banding sites where ratios of HY : AHY birds tend be much lower than at coastal sites (see Nisbet et al. 1963; Ralph 1971, 1981; Hall 1981). High ratios of HY individuals at a site are typically explained as indicating either disorientation of young birds at the periphery of their species' migratory route (Ralph 1981), the selection by inexperienced immatures of lower quality stopover habitat caused by en-route energetic constraints (Moore and Simons 1992), or avoidance of resource competition with adults (Yong et al. 1998). Because many of the transient species (and breeding species consisting largely of presumed transient individuals) captured on Mt. Mansfield are also common coastal migrants (Murray 1966, Ralph 1981, Morris et al. 1996), it is unlikely that Mt. Mansfield constitutes either the eastern or western edge of their migration routes. It seems more likely that young birds might settle on the Mt. Mansfield ridgeline after a nocturnal flight because their energy reserves are depleted, weather conditions inhibit further flights in search of more suitable habitats, or they are inexperienced in selecting optimal stopover habitat. We believe that AHY birds of species not adapted to montane fir-spruce forests may avoid the Mt. Mansfield ridgeline as a stopover habitat because they are less energetically constrained than immatures, more familiar with resource and weather limitations of montane forests, more familiar with the availability of nearby suitable habitats, or more efficient in searching for those habitats.

Recapture rates.—We obtained extremely low recapture rates on Mt. Mansfield, especially among transient species. The overall recapture rate of 1.8% among all species (0.3% among transients) is much lower than that reported during fall from other eastern U.S. banding operations, both inland [e.g., 29.7% at VINS in 1995–1997 (Rimmer, Faccio, and McFarland, unpubl. data); 12.1% at Powdermill in 1995–1997 (Mulvihill and Leberman, pers. comm.); 6.4% at Braddock Bay Bird Observatory in 1995–1997 (Brooks 1996, 1997, 1998)] and coastal [e.g., 30.2% in southeastern Massachusetts in 1995–1997 (Lloyd-Evans, pers. comm.), 13.4% on Appledore Island off New Hampshire (Morris et al. 1996), and ca 10% in Alabama (Woodrey and Moore 1997)]. While recapture data are not strictly comparable among these sites because of differences in seasonal and daily timing of mist-netting operations, number and placement of nets, habitat structure, and other variables, we believe that they highlight the fact that very few transient birds remain on the Mt. Mansfield ridgeline for more than one day after their original capture.

We suggest that conditions on the Mt. Mansfield ridgeline are not conducive to prolonged migratory stopovers in that most migrants are unable to meet their energetic requirements for continued migration at the site. Although migrants approaching the ridgeline at dawn with depleted energy reserves may have few options other than to stop over, the low probability of replenishing or accumulating additional fat reserves may select for short lengths of stay (Rappole and Warner 1976, Terrill 1988, Kuenzi et al. 1991, Moore and Simons 1992). Diminishing insect food supplies and rapidly deteriorating weather during fall probably reduce the suitability of montane fir-spruce habitat for most transients, especially those that are unfamiliar with the habitat. We detected few large fat loads among the birds we examined; nearly half of the recaptured individuals of all migrant classes lost weight and most maintained or lost subcutaneous fat. We believe that most migrants leave the Mt. Mansfield ridgeline shortly after arrival because they encounter few opportunities to satisfy their energy demands.

We do not know whether the presumed rapid departures of most migrants from Mt. Mansfield were due to the initiation of nocturnal migratory flights or to downslope movements in search of more suitable habitats, or both. At Allegheny Front, where the great majority of birds captured are known transients, recapture rates are also extremely low (Hall, pers. comm.). However, Allegheny Front primarily samples migrants that are undergoing active diurnal flights and rarely stop over in the stunted, spruce-dominated ridgeline forest (Hall and Bell 1981). At Mt. Mansfield, the paucity of recaptures and the lack of any detectable diurnal flight suggest a gradual movement away from the ridgeline, possibly to lower elevations. Multiple banding sites across an elevational gradient on Mt. Mansfield's slopes, in combination with radio telemetry, would be necessary to examine this.

Black-throated Blue Warbler.—The disproportionate abundance of Black-throated Blue Warblers in our sample and the high ratio of immatures to adults, suggest that montane fir-spruce forests may be actively selected by juveniles of this species for stopover, postfledging dispersal, or both. The concentration of captures (57%) in August, before the peak of southward departure from northern New England (Holmes 1994), may indicate a pronounced upslope movement away from natal territories in lower elevation northern hardwood forests. While no published information on postfledging dispersal in this species exists, young Black-throated Blue Warblers from first or early season nests are reported to regularly disappear from their natal territories 3–4 weeks after fledging (Holmes, pers. comm.). Black-throated Blue Warblers breed at fairly high densities in northern hardwood forests of northern New England (Holmes et al. 1986, 1996), and nearly half of females are multiple-brooded (Holmes et al. 1992). Independent young from early broods may be competitively excluded from occupied territories of pairs with later nests. Regular upslope movements would take many young Black-throated Blue Warblers into montane fir-spruce forests, where intraspecific competition from territorial adults would be absent. It has been suggested that regular postfledging dispersal of Wood Thrushes to habitats different from those on their natal territories may be driven in part by avoidance of such competition (Anders et al. 1998, Vega Rivera et al. 1998). In mountainous areas of western North America, regular late summer and autumn upslope movements of non-local breeding species, mostly immature birds, are well-documented (Packard 1946, Dixon and Gilbert 1964, Pattie and Verbeek 1966) and may be mediated through competition with adults.

Other possible causes of extensive postfledging movements in Black-throated Blue Warblers might include initiation of migration, socialization, and optimal foraging (see Vega Rivera et al. 1998), but none of these seem likely. Immature Black-throated Blue Warblers do not, to our knowledge, regularly appear at sites south of their main breeding areas or at autumn migration banding sites prior to the species' peak of migratory movement (see Fig. 1; Leberman 1976, Hall 1981, Holmes 1994). Dispersal of young birds to facilitate socialization in conspecific groups (Morton 1991) is not supported by our observational or banding data; most Black-throated Blue Warblers were captured singly or in flocks of 2–3 birds, and none was known to remain on the site for more than one day after initial capture. The lack of recaptures and the low initial fat scores of most Black-throated Blue Warblers in our sample also argue that location of optimal foraging habitat does not drive the dispersal of immatures into Mt. Mansfield's montane forests. We suspect that the altitudinal dispersal of young Black-throated Blue Warblers is driven by competition with adults, and that upslope movements may offer the most rapid means to reach forested habitats free from these competitive constraints.

The apparently rapid departure of immature Black-throated Blue Warblers from a habitat that they appear to select is puzzling. Whether birds continue to disperse or begin to migrate southward along the north–south running ridgelines of the Green Mountains is unknown. A reverse downslope movement back into northern hardwood forests or other lowland habitats seems unlikely. Few HY Black-throated Blue Warblers are observed or captured on long-term study plots in unfragmented northern hardwood forests of New Hampshire during late summer (Holmes, pers. comm.). At VINS, few individuals of this species have ever been captured during the postfledging period over 15 years of banding (Rimmer, Faccio, and McFarland, unpubl. data). The relatively high proportion of Black-throated Blue Warblers captured at Allegheny Front (13.6% of nearly 50,000 wood warblers banded from 1958–1980, third in overall abundance among 33 warbler species; Hall and Bell 1981) and the relatively high proportion of adults at this site, suggest a fall migration route concentrated along the Appalachian Mountains. This is supported by comparatively low capture rates and high HY ratios of this species at the lowland Powdermill site only 130 km north of Allegheny Front (Mulvihill and Leberman, pers. comm.) and at most coastal banding stations (Murray 1966, Ralph 1981, Stewart 1986). We suspect that most individuals captured on Mt. Mansfield continue to move southward along the Green Mountains. More research, incorporating radio telemetry of postfledging birds from known natal sites, is needed to examine this phenomenon.

Conservation implications.—Although the Mt. Mansfield ridgeline and other montane forest sites in eastern North America may not provide optimal stopover habitat for most passage migrants and dispersing juveniles, we believe that the importance of these sites should not be overlooked. Degradation of high elevation habitat "islands" such as Mt. Mansfield could have adverse consequences not only for breeding populations of rare and potentially vulnerable species like Bicknell's Thrush (Rosenberg and Wells 1995, Atwood et al. 1996, Rimmer 1996), but for populations of migrants and postbreeding dispersers as well. Conservation measures that focus on stopover habitat requirements must take into account the diversity of habitat types, and the timing of their use, at all stages between migrants' departure from their breeding territories and arrival on their wintering grounds. We believe that further studies of stopover habitat use in montane forests are warranted and that conservation planning for montane forest sites should carefully consider the needs of migrants outside the breeding season.

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APPENDIX. Summary of fall captures (1995–1997) on Mt. Mansfield, Vermont for species represented by 5 or more individuals.

Species	Migrant class[a]	Captures	% Recaptured	% HY[b]	Range of dates	Median date
Ruby-throated Hummingbird (*Archilochus colubris*)	T	5	unknown[c]	not aged[c]	9 Aug–5 Sep	26 Aug
Downy Woodpecker (*Picoides pubescens*)	T	7	0.0	66.7	3 Aug–11 Oct	19 Sep
Blue-headed Vireo (*Vireo solitarius*)	T	6	0.0	100	21 Aug–19 Sep	12 Sep
Red-eyed Vireo (*Vireo olivaceus*)	T	24	0.0	100	8 Aug–9 Oct	8–9 Sep
Blue Jay (*Cyanocitta cristata*)	S	13	0.0	76.9	9–27 Sep	19 Sep
Black-capped Chickadee (*Poecile atricapillus*)	S	49	12.2	89.1	7 Aug–7 Oct	19 Sep
Red-breasted Nuthatch (*Sitta canadensis*)	B	27	0.0	66.7	1 Aug–9 Oct	7 Sep
Brown Creeper (*Certhia americana*)	B	13	0.0	70	26 Aug–10 Oct	24 Sep
Winter Wren (*Troglodytes troglodytes*)	B	8	0.0	87.5	6 Aug–8 Sep	20 Aug
Golden-crowned Kinglet (*Regulus satrapa*)	B	133	0.0	97.5	6 Aug–12 Oct	27 Sep
Ruby-crowned Kinglet (*Regulus calendula*)	S	207	1.4	71.3	7 Aug–13 Oct	29 Sep
Veery (*Catharus fuscescens*)	T	6	0.0	100	8 Aug–1 Oct	8–9 Sep
Bicknell's Thrush (*Catharus bicknelli*)	B	53	15.1	65.4	1 Aug–2 Oct	11 Sep
Swainson's Thrush (*Catharus ustulatus*)	B	32	0.0	71.9	6 Aug–30 Sep	6 Sep
Hermit Thrush (*Catharus guttatus*)	S	28	0.0	64.3	5 Aug–13 Oct	19–20 Sep
American Robin (*Turdus migratorius*)	B	23	4.3	61.1	5 Aug–13 Oct	15 Aug
Tennessee Warbler (*Vermivora peregrina*)	T	14	0.0	57.1	1 Aug–28 Sep	13–14 Sep
Nashville Warbler (*Vermivora ruficapillus*)	B	31	0.0	90	20 Aug–29 Sep	5 Sep
Chestnut-sided Warbler (*Dendroica pennsylvanica*)	T	16	0.0	100	15 Aug–6 Sep	20–21 Aug
Magnolia Warbler (*Dendroica magnolia*)	B	54	0.0	90.7	8 Aug–29 Sep	30 Aug
Black-throated Blue Warbler (*Dendroica caerulescens*)	T	338	0.0	97.0	2 Aug–9 Oct	29 Aug
Yellow-rumped Warbler (*Dendroica coronata*)	B	754	1.3	89.2	1 Aug–13 Oct	15 Sep
Black-throated Green Warbler (*Dendroica virens*)	T	49	0.0	85.7	3 Aug–6 Oct	5 Sep
Blackburnian Warbler (*Dendroica fusca*)	T	20	0.0	100	9 Aug–19 Sep	30 Aug
Bay-breasted Warbler (*Dendroica castanea*)	T	8	0.0	87.5	7 Aug–13 Sep	7–8 Sep
Blackpoll Warbler (*Dendroica striata*)	B	414	1.7	71.9	1 Aug–9 Oct	5 Sep
Black-and-White Warbler (*Mniotilta varia*)	T	12	0.0	100	3 Aug–11 Sep	19 Aug
American Redstart (*Setophaga ruticilla*)	T	17	0.0	82.4	3 Aug–13 Sep	14 Aug

APPENDIX. CONTINUED

Species	Migrant class[a]	Captures	% Recaptured	% HY[b]	Range of dates	Median date
Ovenbird (*Seiurus aurocapillus*)	T	62	0.0	98.3	3 Aug–28 Sep	22 Aug
Canada Warbler (*Wilsonia canadensis*)	T	31	0.0	86.7	5–30 Aug	15 Aug
Scarlet Tanager (*Piranga olivacea*)	T	5	0.0	100	8 Aug–9 Sep	23 Aug
Lincoln's Sparrow (*Melospiza lincolnii*)	T	5	40.0	80	6–21 Sep	9 Sep
White-throated Sparrow (*Zonotrochia albicollis*)	B	188	3.7	73.2	1 Aug–13 Oct	20 Sep
White-crowned Sparrow (*Zonotrichia leucophrys*)	T	6	0.0	50	20 Sep–13 Oct	29 Sep
Dark-eyed Junco (*Junco hyemalis*)	B	303	3.6	80.7	1 Aug–13 Oct	19 Sep
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	T	11	0.0	100	8–30 Aug	16 Aug
Purple Finch (*Carpodacus purpureus*)	B	6	0.0	50	5 Aug–7 Oct	13 Aug
Class B	B	2044	2.1	81.8	1 Aug–13 Oct	13 Sep
Class S	S	307	2.9	75.3	5 Aug–13 Oct	27 Sep
Class T	T	673	0.3	93.6	1 Aug–13 Oct	28 Aug
Total Captures	All	3024	1.8	84	1 Aug–13 Oct	

[a] Species' status at this site: B = regular breeder above 915 m elevation, S = sporadic/low density breeder above 915 m, T = transient above 915 m elevation.

[b] HY = hatching-year.

[c] Hummingbirds were not banded or processed.

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RANGE EXTENSIONS OF BIRDS IN SOUTHEASTERN AMAZONIA

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ABSTRACT.—We report range extensions of *Caprimulgus sericocaudatus, Automolus ochrolaemus, Dichrozona cincta, Poecilotriccus andrei, Ramphotrigon fuscicauda, Ramphotrigon megacephala, Turdus lawrencii,* and *Euphonia chrysopasta* for Pinkaiti and Gorotire, east of the Xingu River, southeastern Pará State, Brazil. The distributional status of the following species in southeastern Amazonia is also discussed: *Nonnula ruficapilla, Synallaxis cherriei,* and *Simoxenops ucayalae.* The new records we report suggest that the patchy distribution of some birds in eastern Amazonia, such as species associated with bamboo, can be explained by a complex mosaic of habitats at the eastern and southern fringes of the Amazonian basin. The range extensions we report demonstrate that areas inventoried a long time ago, before an emphasis on vocal identification of species, and assumed to be "well known", can in fact turn out to be ornithologically undersampled. *Received 5 April 1999, accepted 30 Oct. 1999.*

RESUMO.—Registramos extensões de distribuição para o sudeste da Amazônia, localidades de Pinkaiti e Gorotire, oeste do rio Xingu, estado do Pará, para as seguintes espécies: *Caprimulgus sericocaudatus, Automolus ochrolaemus, Dichrozona cincta, Poecilotriccus andrei, Ramphotrigon fuscicauda, Ramphotrigon megacephala, Turdus lawrencii* e *Euphonia chrysopasta.* Também discutimos registros para o sudeste da Amazônia das seguintes espécies: *Nonnula ruficapilla, Synallaxis cherriei,* e *Simoxenops ucayalae.* A distribuição de habitats na forma de mosaicos no leste e sul da Amazônia pode explicar a distribuição localizada de algumas espécies de aves na região, como espécies associadas à manchas de taboca. Nossas extensões de distribuição demonstram que áreas na Amazônia exploradas há muito tempo, antes do estudo e documentação acústica da avifauna, e consideradas bem conhecidas ornitologicamente, são na realidade ainda sub-amostradas.

The bird fauna of eastern Amazonia have been surveyed since the beginning of the 1900s (Snethlage 1914, Griscom and Greenway 1941, Novaes 1960). Nevertheless, range extensions of many species and even descriptions of new species and subspecies continue to be reported recently for eastern Amazonia (Graves and Zusi 1990, Novaes 1991, Silva et al. 1995) revealing an incomplete knowledge of the regional avifauna. Here we report range extensions and noteworthy records of birds from two sites in southeastern Amazonia located within the Kayapó Indigenous Reserve. These sites, known as Pinkaiti and Gorotire, are between the rivers Xingu and Araguaia/Tocantins, southeastern Pará State, Brazil (Fig. 1). Most of our records represent range extensions into the Xingu River drainage and several are the first reports from the State of Pará, Brazil.

METHODS AND STUDY AREA

The first site surveyed was Gorotire (07° 43′ S, 51° 11′ W), on the banks of Fresco River, an eastern tributary of the Xingu River, in the ecological transition zone between evergreen and semideciduous forests and cerrado. For details on the vegetation types found in this site see Oren and Silva (1987). The second site we surveyed, about 150 km northwest of Gorotire, is known locally as Pinkaiti (07° 46′ S, 51° 58′ W, about 360 m elevation, on the right bank of Riozinho River, a second-order eastern bank tributary of the Xingu River). This area is approximately 20 km upstream on the Riozinho River from the Kayapó village of A'ukre in the northern sector of the Kayapó Indigenous Reserve. From an avifaunal perspective, Pinkaiti comprises three major habitats: the river itself, forest and "viny" bamboo on the river floodplain, which at the study site is about 200 m wide; and terra firme forest. Forest in the area is largely undisturbed, although selective logging in the immediate vicinity of the study site has left numerous canopy light gaps and some patches of extensive brushy growth. Narrow trails provide limited access to all habitats (the dominant habitat, terra firme forest, is transected by several good trails). The terra firme forest at Pinkaiti is classified as open terra firme forest (high structural heterogeneity with small cerrado enclaves), a vegetation type characteristic of the dry-belt arch of transitional forest mosaic of southern Amazonia (Pires and Prance 1985). For a descriptive account on the vegetation of Pinkaiti see Peres and Baider (1997).

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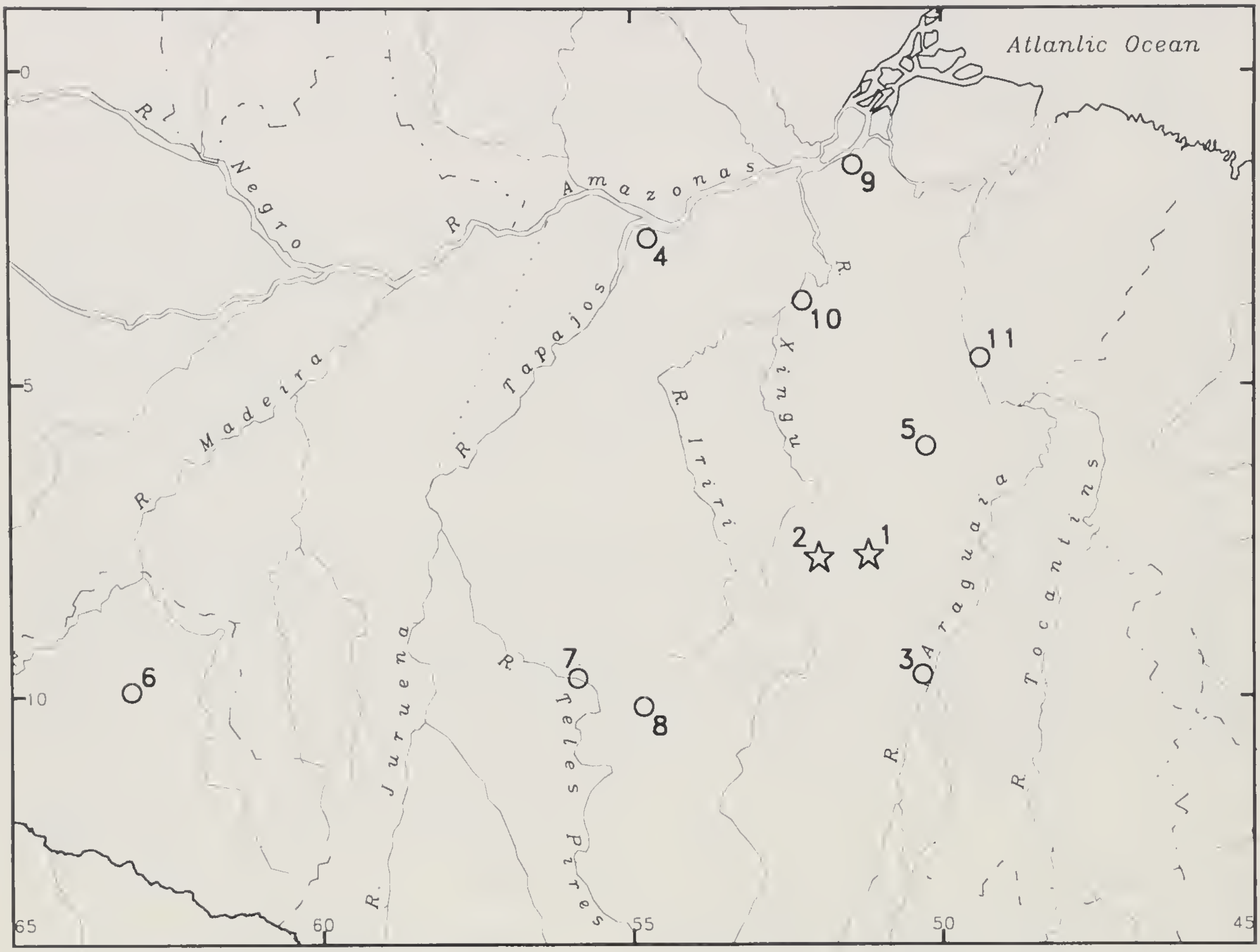

FIG. 1. Localities in the Brazilian Amazon with coordinates cited in the text. Stars denote localities visited by the authors, whereas circles depict those localities cited in the literature or available from material deposited at the ornithological collection of the Museu Paraense Emílio Goeldi, Belém, Pará, Brazil. 1 = Gorotire, PA; 2 = Pinkaiti, PA; 3 = Santana do Araguaia, PA; 4 = Santarém, PA; 5 = Serra dos Carajás, PA; 6 = Fazenda Rancho Grande, Ariquemes, RO; 7 = Alta Floresta, MT; 8 = Peixoto de Azevedo, MT; 9 = Caxiuanã National Forest, PA; 10 = Altamira, PA; 11 = Jacundá, PA.

Field work at Gorotire was carried out by D.C.O. from 6–27 September 1983 and from 16 May to 6 June 1985. Specimens were collected with shotgun and mist-nets, and deposited in the bird collection of the Museu Paraense Emílio Goeldi, Belém, Pará, Brazil (hereafter MPEG). Pinkaiti has been an active research site of Conservation International, Washington, D.C. for several years, and most of A.A.'s and B.M.W.'s observations were made within a few kilometers of this base camp. Field work, mostly on foot, by A.A. and B.M.W. was carried out during three periods: 22–26 September 1994, 22–27 September 1995 (B.M.W.), and 5 September–3 October 1996 (A.A.). A small sample (36 specimens) of selected taxa was collected with a shotgun and 12 m mist-nets by B.M.W. and D. Pimentel Neto of the MPEG during 1995. These specimens are deposited in the museum. Tape recordings by A.A. are deposited at Arquivo Sonoro Neotropical (ASN, Campinas, Brazil) and Library of Natural Sounds, Cornell Laboratory of Ornithology (LNS), Ithaca, New York. B.M.W.'s tape recordings are or will be deposited at Arquivo Sonoro Elias P. Coelho (ASEC, UFRJ, Rio de Janeiro, Brazil) and LNS. Field observations and specimens collection at the study sites were supplemented with study of specimens from different localities throughout southeastern Amazonia deposited at the MPEG.

For passerine birds, we followed the nomenclature and English names adopted by Ridgely and Tudor (1989, 1994). Meyer de Schauensee (1982) was the source of non-passerine Latin and English names. Localities with coordinates mentioned in the text are depicted in Fig. 1.

SPECIES ACCOUNTS

Silky-tailed Nightjar, Caprimulgus sericocaudatus.—This poorly known caprimulgid was observed and tape recorded in terra firma forest at Pinkaiti during all three visits. Individuals sang from perches within 1.5 m of the ground (but not on the ground) along trails and in small understory openings. Foraging moves shortly after dark were rapid upward sallies of 2–3 m from the same low perches as used for singing. Several birds responded agressively to tape recorded playback in September. Only one other record of this nightjar is available for eastern Amazonia, a specimen from Santarém, Pará (02° 26′ S, 54° 42′ W; Griscom and Greenway 1941), situated on the right bank of the Tapajós River near its mouth. Our records extend the range of this nightjar about 480 km southeastward, indicating a large distributional range in the lower Amazonian basin. Other Amazonian records are clustered in eastern Peru: Pucallpa and Yarinacocha (Loreto Department; Dickerman 1974), Manu National Park (J. Arvin, pers. comm.), Tambopata (Mcquenn, pers. comm.), northern Bolivia: Río Heath (Parker et al. 1991), and Tuichi River in Madidi National Park, La Paz Department (B.M.W., pers. obs.). Tape recordings of birds from Pinkaiti and widely disjunct eastern Peru and northern Bolivia sound quite similar (B.M.W., pers. obs.), but have not been examined in detail.

Rufous-capped Nunlet, Nonnula ruficapilla.—Novaes (1991) first reported this species east of the Xingu River, at Jacundá (4° 35′ S, 49° 34′ W; eastern bank of the Tocantins River), Pará and assigned it to a new subspecies (*N. r. inundata*). Additional specimens assignable to *N. r. inundata* were collected (June and August 1992) by D.C.O. and D. Pimentel Neto farther south at Santana do Araguaia (9° 50′ S, 50° 15′ W; MPEG 48564–48566; two males, one female, all adults not actively reproductive when collected). This species seems to be uncommon at Pinkaiti, although it was noted during all three surveys (tape-recorded by B.M.W.). It inhabits both terra firme and river-edge forest, in or near dense subcanopy vine tangles, especially around treefalls and other light gaps. It has been found in a similar habitat along the Parauapebas River at the foot of the Serra dos Carajás (6° 00′ S, 51° 20′ W; B.M.W., pers. obs.) and at Fazenda Rancho Grande, near Ariquemes (9° 56′ S, 63° 04′ W), Rondônia (Zimmer et al. 1997). In the Alta Floresta region of northern Mato Grosso (9° 41′ S, 55° 54′ W), *N. ruficapilla* has been found in bamboo thickets and in vine-rich terra firme forest without bamboo (Zimmer et al. 1997). Novaes and Lima (1990) provided no data on habitat utilization for *N. ruficapilla* in the lower Rio Peixoto de Azevedo region (10° 10′ S, 54° 50′ W), about 390 km southwest of Pinkaiti. Although it may be closely associated with bamboo locally, in northern Amazonian Peru south of the Marañon River, *N. ruficapilla* inhabits seasonally flooded and lake-edge forest with no bamboo present (B.M.W., pers. obs.).

Chestnut-throated Spinetail, Synallaxis cherriei.—The Chestnut-throated Spinetail was a common bird at forest edges and around tangled treefalls in terra firme forest at Pinkaiti. We observed the species in the same types of habitats described by Oren and Silva (1987) in eastern Amazonia, near Gorotire. Zimmer and co-authors (1997) reported that *S. cherriei* was restricted to stands of bamboo in the Alta Floresta region and that the presumably closely related Ruddy Spinetail (*S. rutilans*) inhabited dense tangles in forest interior light-gaps. Both species are sympatric at Serra dos Carajás (6° 00′ S, 51° 20′ W), where they are uncommon around dense treefalls and other tangled vegetation, neither appearing to be restricted to bamboo (B.M.W, pers. obs.).

Peruvian Recurvebill, Simoxenops ucayalae.—This species was first reported for two locations of southeastern Amazonia by Sick (1997): Serra dos Carajás and Gorotire. These records are incorrectly based on Oren and Silva (1987), who dealt exclusively with the distribution of *Synallaxis cherriei* and not *Simoxenops ucayalae.* There are no known field records or specimens of *S. ucayalae* for Gorotire (Novaes 1960). Sick's (1997) citation is based on an adult male collected on 19 May 1986 at Pojuca, in the Serra dos Carajás area (6° 00′ S, 51° 20′ W) deposited at MPEG (38156; mass 50 g; gonads 5 × 3 mm) and reported to him by D.C.O.

The Peruvian Recurvebill has also been reported for Altamira in the lower Xingu River (3° 39′ S, 52° 22′ W; Graves and Zusi 1990), about 250 km northwest of Serra dos Carajás, and Alta Floresta (9° 41′ S, 55° 54′ W; Zimmer et al. 1997). Another eastern Amazonian specimen, from Santarém (MPEG 32018), is thought to be mislabeled (Novaes 1978). Novaes (1978) considered that this specimen probably came from Acre state instead of Santarém because up to that date, the only records available for this species in Amazonia were from southeastern Peru (upper Río Ucayali and Madre de Dios; Meyer de Schauensee 1982), close to the border with the Brazilian state of Acre. The well documented records of Serra dos Carajás and Altamira prove unequivocally that *S. ucayalae* occurs, at least locally, in eastern Amazonia. Thus, it is possible that the record of *S. ucayalae* for Santarém (roughly 230 km west of Altamira) is correct.

Buff-throated Foliage-gleaner, Automolus ochrolaemus.—This is the first published report of this species for the Xingu River drainage. Three specimens assignable to the subspecies *auricularis* were collected in 1985 near Gorotire by D.C.O. and D. Pimentel Neto (MPEG 37074–37076). A.A. tape recorded and B.M.W. observed pairs of this foliage-gleaner as they accompanied mixed-species flocks in the understory of terra firme forest in Pinkaiti. Three more recent specimens from the Xingu River drainage (MPEG 48717–48719) were collected in 1992 at Santana do Araguaia, about 250 km southeast of Pinkaiti.

This species is distributed widely, from Central America to Amazonia on both sides of the Solimões-Amazonas rivers (Meyer de Schauensee 1982, Ridgely and Tudor 1994). South of the Solimões-Amazonas rivers, the easternmost population reported previously (*A. o. auricularis*) inhabits the lower Peixoto de Azevedo River region (10° 10′ S, 54° 50′ W) in northern Mato Grosso (Novaes and Lima 1990), about 390 km southwest of Pinkaiti. This foliage-gleaner was classified as uncommon to fairly common around Alta Floresta, near the head of the Tapajós drainage (Zimmer et al. 1997).

Despite fairly extensive coverage, *A. ochrolaemus* has not been recorded in the Serra dos Carajás area (Pacheco and Fonseca, unpubl. data; M. Cohn-Haft, pers. comm.). Our field observations and the habitat information recorded on labels of the three specimens collected in Santana do Araguaia, suggest that this species may be linked to riverine habitats in eastern Amazonia.

Banded Antbird, Dichrozona cincta.—Our only record was of a single individual tape recorded and observed in lightly disturbed terra firme forest at Pinkaiti on 24 September 1994. B.M.W. also tape recorded and observed this species at the Ferreira Penna Scientific Station of the MPEG in the Caxiuanã National Forest (1° 24′ S, 51° 27′ W) on 30 May 1997, where specimens were collected by Silva (1998). These appear to be the only records east of the Xingú River (Griscom and Greenway 1941, Sick 1997). Among sites across southeastern Amazonia, Alta Floresta seems to have been inventoried most thoroughly and the apparent absence of *D. cincta* in this area may be real (Zimmer et al. 1997).

Black-chested Tyrant, Poecilotriccus andrei.—A rare and patchily distributed bird in Amazonia (see summary in Sick 1997), with most records coming from the eastern part of the basin, which seems to be the species' stronghold (Novaes 1978, Sick 1997). A.A. saw one female at Pinkaiti, identified by its distinct blackish crest and wide yellowish band across primaries, secondaries, and tertiaries. The bird was perched quietly for 30 s about 1.5 m above ground in a large forest gap dominated by vine-tangles. This is the southernmost record so far reported for this species. *Poecilotriccus andrei* has been also collected at Serra dos Carajás (MPEG 37287; no mass or gonad information), about 200 km northeast of Pinkaiti.

Large-headed Flatbill, Ramphotrigon megacephala.—On 27 May 1985, a female was collected by D.C.O. and M. S. Brígida in Gorotire (MPEG 37170; mass 12.5 g; small gonads). The bird was found in a bamboo patch surrounded by secondary forest. This represents the first published record of *R. megacephala* for eastern Amazonia and Pará State. Like *R. fuscicauda,* the nearest locality where *R. megacephala* has been reported previously is Alta Floresta in northern Mato Grosso State (9° 41′ S, 55° 54′ W; Aleixo 1997), 490 km southwest of Gorotire.

Dusky-tailed Flatbill, Ramphotrigon fuscicauda.—This species was tape recorded in 1995 and 1996 at Pinkaiti (B.M.W. and A.A.), providing the first documented records for Pará and the Xingu River drainage. The nearest locality where this flatbill had been reported previously is Alta Floresta, about 450 km southwest of Pinkaiti, where it was considered a bamboo specialist (Zimmer et al. 1997). The Dusky-tailed Flatbill is an uncommon bird at Pinkaiti, inhabiting dense places in the upper understory (generally 2–6 m above ground) of terra firme and floodplain forest, often near trail edges or other light gaps. Over most of its wide but patchy distribution, *R. fuscicauda* is found in but not restricted to bamboo (Parker et al. 1997, Kratter 1997).

Lawrence's Thrush, Turdus lawrencii.—This forest thrush was tape recorded and collected at Pinkaiti (MPEG 52326) by B.M.W. on 25 September 1995, providing the first report for Pará and the Xingu River drainage. Another individual was heard singing nearby. The nearest locality where this bird had been ereported was in the lower Peixoto de Azevedo River region (10° 10′ S, 54° 50′ W), upper Tapajós River drainage, in northern Mato Grosso (Novaes and Lima 1990). It was considered uncommon at nearby Alta Floresta region (Zimmer et al. 1997).

White-lored Euphonia, Euphonia chrysopasta.—An individual tape recorded and briefly seen by A.A. at Pinkaiti on 25 September 1996 is the only record of this species from the Xingu River drainage. The only records from farther east are from the plateau region of Serra dos Carajás (B.M.W. and R. Webster, pers. obs.), 200 km northeast of Pinkaiti. The nearest documented record for this euphonia comes from the lower Peixoto de Azevedo River region (10° 10′ S, 54° 50′ W), upper Tapajós River drainage, where one specimen was collected (Novaes and Lima 1990).

DISCUSSION

The range extensions we report and those reported elsewhere for eastern Amazonia (Oren and Silva 1987, Graves and Zusi 1990, Novaes 1991) reveal an incomplete knowledge of bird distributions in this region, despite previous work by earlier authors (Snethlage 1914, Griscom and Greenway 1941, Novaes 1960). Many of the range extensions are for species of more widespread distribution in western Amazonia, such as *Caprimulgus sericocaudatus, Simoxenops ucayalae, Dichrozona cincta, Ramphotrigon fuscicauda, R. megacephala, Turdus lawrencii,* and *Euphonia chrysopasta.*

Most of Amazonia on the Brazilian Shield is comprised of seasonally semideciduous and evergreen forests, dominated by *Orbingyia* palms and lianas (RADAMBRASIL satellite imagery data in Prance and Brown 1987). This region includes a highly complex mosaic of biotopes, including scattered enclaves, some extensive, of cerrado, bamboo, campinas, and gallery forest. This mosaic is characteristc of the broadly defined Transition forest (sensu Prance and Brown 1987) at the southern periphery of Amazonia.

The patchy distribution of the different habitats comprising Transition forest in eastern Amazonia may account for the localized occurrence of some species. Species like *Simoxenops ucayalae, Ramphotrigon fuscicauda,* and *R. megacephala* are reported to be highly associated with *Guadua* spp. bamboo patches in western Amazonia (Kratter 1997, Parker et al. 1997). In southwestern Amazonia, bamboo dominated forests cover an extensive and rather continuous area of aproximately 180,000 km^2, about evenly divided between Brazil and Peru (Nelson 1994). In contrast, patches of bamboo are less numerous and more locally distributed in southeastern Amazonia in general (RADAMBRASIL satellite imagery data in Prance and Brown 1987). This may explain why bamboo associated species have a patchier distribution in eastern than western Amazonia.

Our records of "obligate" and "near-obligate" bamboo specialist birds (sensu Kratter 1997), such as *Nonnula ruficapilla* and *Ramphotrigon fuscicauda,* in vegetation other than *Guadua* spp. bamboo patches, also demonstrate that the degree of association with *Guadua* bamboo can vary geographically in Amazonia. Indeed, Kratter (1997) acknowledged that most bamboo specialist birds probably select a particular type of vegetation structure (dense habitats with low canopy cover) rather than a particular floristic component. In areas where *Guadua* stands are rare, such as in southeastern Amazonia, alternative habitats to *Guadua* bamboo can be even more important than in other parts of Amazonia.

The geographic patchiness of habitats within a broad, complex mosaic of biotopes and general ornithological undersampling, account for many range extensions we observed of patchily distributed species in eastern Amazonia. Areas inventoried before an emphasis on vocal identification of species can turn out to be ornithologically undersampled. Continuous field work, combining extensive tape recording with modern collecting (including gathering samples for genetic studies) is needed to obtain a more accurate picture of Amazonian biogeography, and to allow generalizations and modeling.

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Short Communications

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Sex-related Differences in Migration Chronology and Winter Habitat Use of Common Snipe

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ABSTRACT.—There is little information concerning differences in migration chronology between male and female Common Snipe (*Gallinago gallinago*) and virtually no accounts of sex-related differences in winter habitat use. We collected 372 Common Snipe in five different habitat types during the non-breeding period along the central Gulf Coast of Texas. Proportions of male and female snipe collected on wintering areas during the beginning of the fall period (i.e., between 6 and 21 October) indicated a tendency for females to arrive ahead of males. Sex ratios during the latter part of spring (16 March–10 April 1998) suggested male snipe leave wintering areas before females. During the winter period (14 November 1997–4 February 1998), female snipe were more common than males along the Texas Gulf Coast. Differences in sex ratios during winter are likely due to sex-related differences in habitat use. During winter, females were more common than males in heavily vegetated habitats (e.g., coastal marshes and cultivated rice fields). Conversely, males were more common in open habitats (e.g., mud flats). Male snipe may begin spring migration before females to establish territories on the breeding grounds. Sex-specific differences in winter habitat use may be related to reverse sexual size dimorphism of Common Snipe. *Received 16 April 1999, accepted 23 Sept. 1999.*

Among most shorebird species (Charadriiformes), males begin spring migration before females, and females begin fall migration before males (Oring and Lank 1982, 1986; Morrison 1984). These patterns may be reversed depending on the breeding system, type of parental care, molting schedule, or distance to wintering areas for each sex (Oring and Lank 1982, 1986; Pienkowski and Evans 1984). American Woodcock (*Scolopax minor*) do not exhibit sex-related differences in timing of fall migration, but males compete for the best breeding territories and begin spring migration before females (Sepik and Derleth 1993a). In contrast, Spotted Sandpipers (*Actitis macularia*) exhibit resource defense polyandry and females arrive on breeding grounds earlier than males (Oring and Lank 1982, 1986). Previous studies of Common Snipe (*Gallinago gallinago*) have reported dates of migration from breeding and wintering areas (Arnold and Jirovec 1978, Johnson and Ryder 1977, McKibben and Hofmann 1985), but few have reported sex-related differences in arrival and departure times. Whitehead (1965) and Tuck (1972) suggested that male snipe began spring migration before females. However, Whitehead (1965) concluded that males also began fall migration before females, contrary to Tuck's (1972) conclusion.

Although many shorebird species exhibit sex-related differences in habitat use (Puttick 1984), there are no published accounts of such differences for Common Snipe. However, White and Harris (1966) analyzed differences in diets of wintering snipe collected from five different habitats in northern California and concluded there were behavioral differences associated with habitat use among snipe (i.e., they used salt marsh habitat mostly for loafing and upland pastures as feeding sites). In addition, male American Woodcock use forest openings more than females do during summer, fall, and winter (Horton and Causey 1979, Sepik and Derleth 1993b). Because woodcock and snipe are closely related and have similar foraging strategies, we hypothesized that male snipe may use less vegetated habitats than females during the non-breeding period.

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We investigated migration chronology of male and female snipe by comparing sex ratios of snipe collected on wintering areas along the central Gulf Coast of Texas during fall and spring. In addition, we report differences in proportions of males and females collected in five habitat types during the winter period. This study was conducted as part of a larger project to determine methods for externally aging and sexing Common Snipe and to investigate their nutritional ecology (i.e., diet, body composition, and gut morphology) throughout the non-breeding period.

STUDY AREA AND METHODS

We conducted this study in the rice prairies and coastal marshes of Brazoria, Calhoun, Colorado, and Wharton Counties of Texas from October 1997 through April 1998. Collection sites included private farmland, several wildlife management areas (WMA) managed by Texas Parks and Wildlife Department, and Brazoria National Wildlife Refuge (NWR). Collection sites were comprised of five different habitat types including harvested rice fields, mud flats, fallow rice fields, drained impoundments, and coastal marshes. Vegetation in harvested rice fields contained mostly rice (*Oryza sativa*) and ryegrass (*Lolium* spp.) knocked down by Lesser Snow Geese (*Chen caerulescens*) and White-fronted Geese (*Anser albifrons*). Mud flats were recently plowed rice fields that contained no standing vegetation. Fallow rice fields had not been cultivated for three years and contained mostly smartweed (*Polygonum* spp.), false indigo (*Amorpha fruticosa*), and rattlebox (*Sesbania drummondii*). Drained impoundments had not been cultivated for rice production for two years and contained mostly smartweed, rattlebox, broadleaf signal grass (*Brachiaria platyphylla*), false indigo, nutsedge (*Cyperus* spp.), and millet (*Echinochloa* spp.). Coastal marshes had been moderately grazed by cattle and burned in September 1997; dominant vegetation included spike rush (*Eleocharis* spp.), Gulf cordgrass (*Spartina spartinae*), salt grass (*Distichlis spicata*), and marsh-hay cordgrass (*Spartina patens*). With exception of Brazoria NWR, all sites were hunted intensively for waterfowl, but snipe hunting was rare.

We collected snipe by shooting and systematically alternated between habitat types throughout the non-breeding period. To maintain equal sampling effort, we typically collected four birds per day throughout the diurnal period. All specimens were sexed by gonadal examination and we recorded the habitat type from which each bird flushed. We separated the non-breeding period into three seasons, using the period of pre-basic molt to define fall (6 October–13 November 1997), the non-molting period to define winter (14 November 1997–4 February 1998), and pre-alternate molt to define spring (5 February–10 April 1998). These dates are based on physiological events rather than arbitrary calendar dates. We feel they provide a better source of interpretation for detecting physiological (i.e., body composition and gut morphology) and dietary changes in Common Snipe. We used a standard Z-test (SAS version 6.12 for Windows; SAS Institute, Inc. 1988) testing the null hypothesis that proportions of male and female snipe during each seasonal period and within each habitat type during winter were equal to 50%.

RESULTS

Between 6 October 1997 and 19 April 1998, we collected 372 Common Snipe (152 males and 220 females). Females ($n = 25$) were more common than males ($n = 15$) during the first 26 days of the fall period, with sex ratios becoming approximately even (14 females, 15 males) during the last 13 days (Fig. 1). Between 6 and 21 October there appears to be a trend of more females ($n = 15$) than males ($n = 7$; $Z = 1.70$, 1 df, $P = 0.088$). However, proportions of male and female snipe did not depart significantly from an even sex ratio during fall ($Z = 1.58$, 1 df, $P > 0.05$). Sex ratios (45 females, 41 males) during the first 39 days of the spring period were essentially even (Fig. 2). Between 16 March and 10 April, females ($n = 41$) were more common than males ($n = 17$) and proportions departed significantly from a 50:50 sex ratio ($Z = 3.15$, 1 df, $P = 0.002$). Most snipe had left wintering areas along the central Gulf Coast of Texas by 10 April, and none was observed after 19 April, despite daily surveys.

During the winter period, the overall proportion of males ($n = 64$) to females ($n = 95$) departed significantly from an even sex ratio ($Z = 2.46$, 1 df, $P = 0.014$). We excluded 12 males and 17 females from the habitat use analysis because we were unable to determine the habitat type from which they flushed. Sex ratios were skewed toward females in rice fields and coastal marshes, while mud flats contained a higher proportion of males (Table 1). Proportions of male and female snipe were similar in fallow rice fields and drained impoundments (Table 1).

DISCUSSION

We observed few snipe from 6–14 October 1997, but the number of birds gradually increased into November indicating that most snipe arrived on wintering areas along the central Gulf Coast of Texas after mid-October. Arnold and Jirovec (1978) reported that the

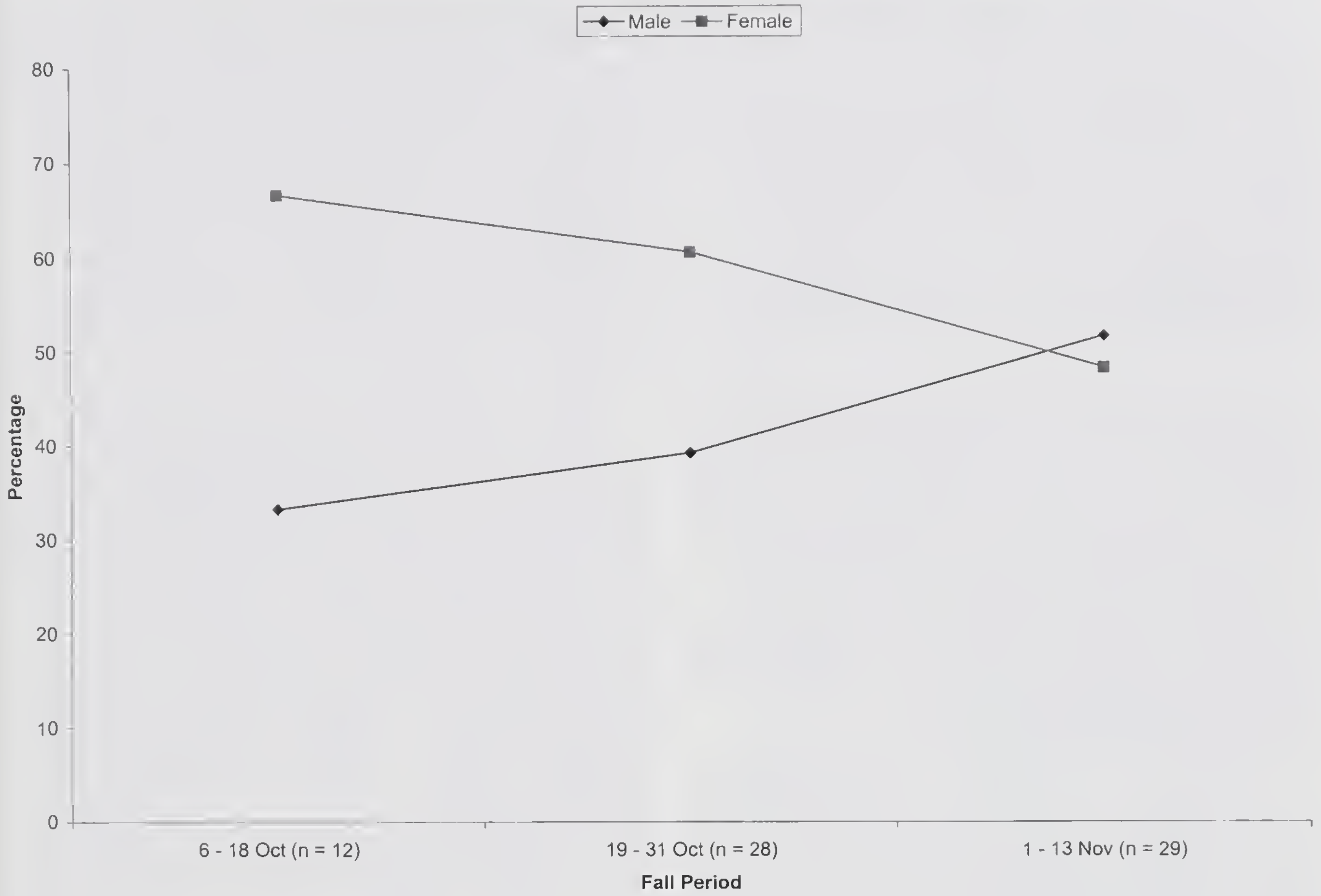

FIG. 1. Proportion of male and female Common Snipe (*Gallinago gallinago*) on wintering areas along the central Gulf Coast of Texas during fall.

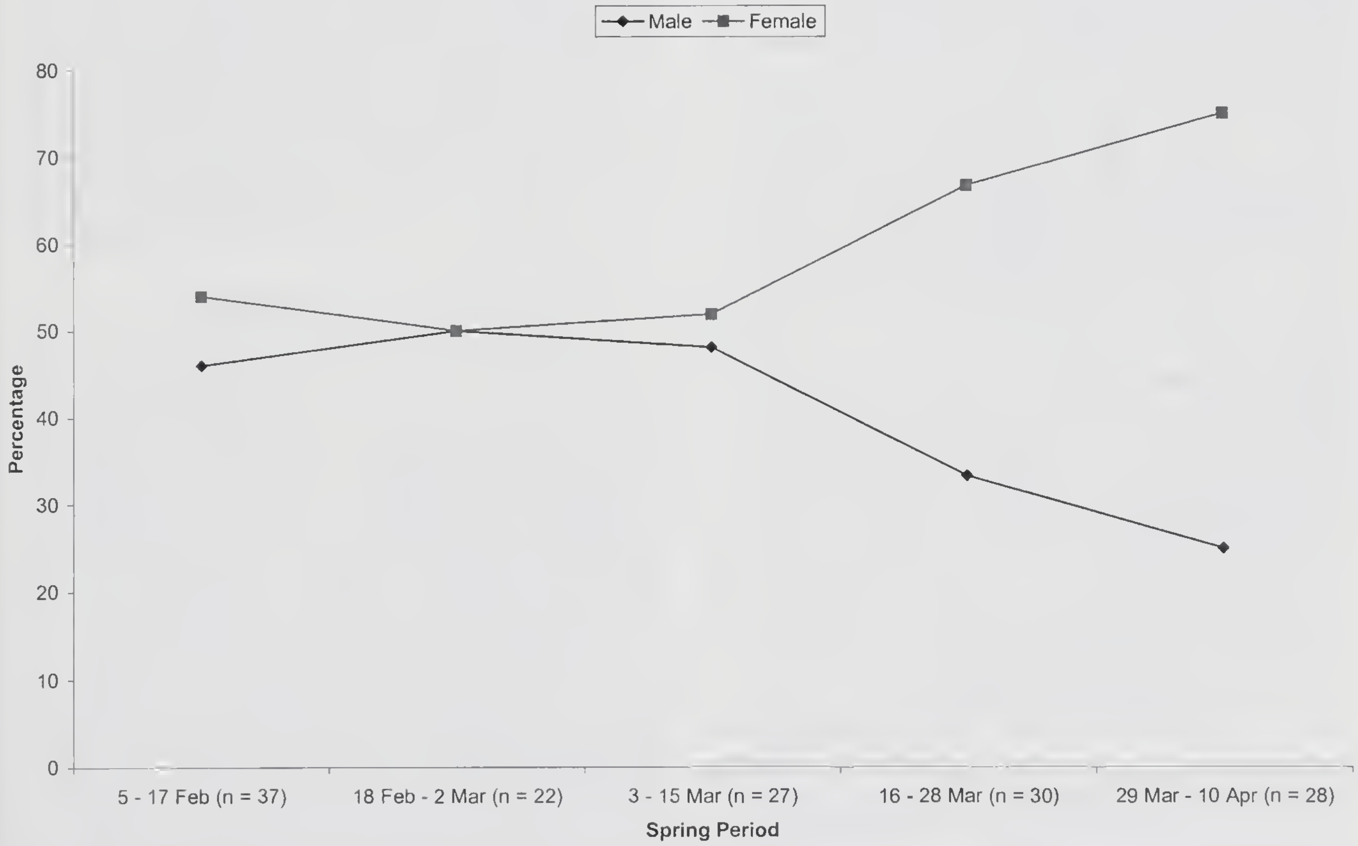

FIG. 2. Proportion of male and female Common Snipe (*Gallinago gallinago*) on wintering areas along the central Gulf Coast of Texas during spring.

TABLE 1. Percent (n) of Common Snipe collected in different habitat types during winter 1997–1998 along the central Gulf Coast of Texas.

Habitat	Male	Female	Z^a	P
Rice field	31.6 (12)	68.4 (26)	2.27	0.023
Mud flat	82.6 (19)	17.4 (4)	−3.13	0.002
Fallow rice field	38.5 (5)	61.5 (8)	0.83	>0.05
Coastal marsh	23.7 (9)	76.3 (29)	3.24	0.001
Drained impoundment	38.9 (7)	61.1 (11)	0.94	>0.05

[a] df = 1.

average fall arrival date of Common Snipe on wintering areas in east-central Texas was 5 October. White and Harris (1966) reported similar arrival dates on wintering areas in northwestern California. Studies conducted on breeding areas in Colorado and California indicate that snipe typically depart around mid-September (Johnson and Ryder 1977, McKibben and Hofmann 1985).

During fall there was no significant difference in the overall proportion of male and female Common Snipe. However, females were more common than males earlier in the fall, suggesting that females arrive on wintering areas before males (Fig. 1). It is possible that birds arriving before mid-October are failed breeders (i.e., both male and female) that are followed by females that have successfully reproduced. This would be consistent with most shorebird species where fall migration sequence is generally: failed breeders→ adult females→ adult males→ juveniles (Oring and Lank 1982, Morrison 1984). Shorebird species that migrate long distances generally exhibit a tendency toward promiscuous breeding systems and one sex (usually the female) departs prior to the sex taking on most or all brood rearing responsibilities (Morrison 1984). Although evidence is lacking, snipe are probably monogamous with females performing incubation and males sharing equally in brood rearing responsibilities (Tuck 1972). However, suspected equality in parental duties among monogamous shorebird species often proves unequal, with males actually assuming most of the brood rearing responsibility (Miller 1985). Desertion by the female may reduce competition for food between the remaining parent and young, while increasing her chance of survival by allowing her to reach staging and wintering areas before prey availability is reduced (Jonsson and Alerstam 1990).

Sex ratios were essentially even from 1–13 November (Fig. 1) and from 5 February to 15 March (Fig. 2), but during winter female snipe were more common than males. It is possible that male snipe winter farther south than females due to their smaller body size (Nichols and Haramis 1980, Arnold 1991). However, our data (Fig. 2) suggest that male Common Snipe (like male American Woodcock) begin spring migration before females, probably to establish breeding territories. Spring migration, intrasexual competition for territories, and courtship displays are stressful activities for male woodcock (and probably snipe as well) and often occur when snow and ice reduce food availability (Owens and Krohn 1973). Because male snipe must reach northern breeding area before females, it does not appear energetically advantageous for males to winter farther south than females considering the relatively mild winters along the central Gulf Coast of Texas. Thus, a more likely explanation for skewed sex ratios during winter is that male and female snipe use different habitats.

Our data show male snipe used open areas more than females, while females used vegetated areas more than males. Similarly, the nocturnal behavior of American Woodcock shows males use forest openings considerably more than females on both wintering and breeding areas (Horton and Causey 1979, Sepik and Derleth 1993b). Sex-specific differences in habitat use may be related to reverse sexual size dimorphism exhibited by Common Snipe. Snipe are tactile feeders, probing moist soil for invertebrates and using low vegetation for escape cover (Arnold 1994). The longer bill of the female may facilitate capture of larger, more nutritious prey found deeper in the soil enabling her to accumulate nutrient reserves needed for egg production more efficiently (Jonsson and Alerstam 1990). On the other hand, if male snipe undertake most parental care, they will likely forage in habitats where their short-billed young can feed efficiently. Thus, they would benefit from a shorter bill themselves while enhancing their parental efficiency (Jonsson and Alerstam 1990). If food is limited, intersexual competition by shorebirds on wintering grounds may be reduced by using different habitats, different size classes of prey, or employing different foraging techniques (Puttick 1978).

In the United States, the largest snipe harvests occur on the wintering grounds of Louisiana, Florida, California, and Texas (Arnold 1994). Although harvests have declined since 1976, poor hunter tracking methods make it difficult to determine if declines are due to fewer snipe hunters, fewer birds, or both (Arnold 1994). Hunter success may be lower in open habitats (i.e., those typically used by males) because snipe tend to flush earlier, out of shotgun range, in these areas compared to more vegetated habitats (J.T.M., pers. obs.). Consequently, wintering female snipe may be more susceptible to harvest than males because of their association with vegetated habitats. Our data suggest that females are more abundant than males, but population managers and ecologists should be aware that obtaining unbiased estimates of true sex ratios for Common Snipe during the non-breeding period might be difficult because of sex-related differences in habitat use.

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Arboreal Nocturnal Roosting Behavior of a Fledgling American Dipper

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ABSTRACT.—Although the American Dipper (*Cinclus mexicanus*) uses a variety of sites on the ground adjacent to streams for nocturnal roosts, I observed nocturnal roosting in a tree by this species, apparently the first reported case for any dipper species. A fledgling spent at least 8 hours between 20:06 and 04:30 MST sleeping 1.5 m high in a black cottonwood tree (*Populus trichocarpa*), at the tip of a branch overhanging a creek. Use of arboreal roost sites may reduce the probability of predation on fledgling dippers while they are sleeping. *Received 1 Aug. 1999, accepted 19 Oct. 1999.*

Sites selected by diurnal birds for nocturnal roosting are no less important for survival than sites they choose for nesting (Skutch 1989) because sleeping birds are extremely vulnerable to predators and unfavorable weather. American Dippers (*Cinclus mexicanus*) are known for a life cycle closely associated with fast-moving water and for placing nests in sites that are inaccessible to most predators, such as stream-side cliffs, midstream boulders, behind waterfalls, and the undersides of bridges (Bent 1948; Kingery 1996; pers. obs.). Adults often roost overnight during the breeding season in or near their nests under bridges and in rock crevices (Kingery 1996), and once were reported roosting during winter under a tangle of roots in a steep stream bank (Ehinger 1930). Nest and nocturnal roost sites similar to those of the American Dipper are used by the ecologically similar Eurasian Dipper (*C. cinclus*; Cramp 1988, Tyler and Ormerod 1994). Recently fledged Eurasian Dippers sometimes return to the nest to roost overnight (Cramp 1988).

Survival estimates for fledgling and juvenile American Dippers are less than 35% (Price and Bock 1983); consequently, choice of nocturnal roost sites could be an important component affecting juvenile survival. I have been unable to locate previous reports of dippers of any species roosting overnight in trees or shrubs. However, perching in vegetation, including trees along streams, has been reported occasionally for American and Eurasian dippers (Drew 1881; Merriam 1899; Bakus 1959; Hewson 1967; S. Osborn, pers. comm.), up to 7.6 m above the ground.

I made the following observation of arboreal roosting by a fledgling American Dipper along West Rosebud Creek at Pine Grove Campground (45° 16′ N, 109° 39′ W; 1798 m elevation) in the Beartooth Mountains of Stillwater County, Montana. At 19:56 MST on 23 June 1999 I heard a fledgling dipper at streamside that vocalized loudly while being fed by an adult. During the next 10 min the fledgling was fed twice as it remained within a 6–8 m stretch of streamside habitat beneath a canopy

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of lodgepole pine (*Pinus contorta*) and black cottonwood (*Populus trichocarpa*). During the same interval, five times the fledgling flew to the lowest branches (< 2 m above ground level) of two cottonwood trees that overhung the stream bank.

On the fledgling's first foray into the trees it continued to dip (a rapid up-and-down movement of the entire body, performed by flexing the legs into a crouch then standing; Kingery 1996), making the branch on which it perched vibrate noticeably. The bird remained in the tree for 45 s before flying back to the bank below the tree. Shortly after returning to the bank it again flew up to the same branch. This time the bird froze in a crouched position as soon as it landed and remained motionless for about 30 s before again returning to the bank below the tree. Shortly after returning to the bank it was fed by an adult. It moved 3 m downstream along the bank before flying clumsily up to the branch of another cottonwood, where it clung upside down for about 5 s before falling into the creek and swimming to shore. The fourth foray up to the cottonwoods was similar to the first, with the fledgling continuing to dip as it stood on a branch in the second cottonwood before once again flying down to the bank below the trees, whereupon it was fed a second time by an adult. At 20:06 the fledgling flew up to the branch where it perched originally and immediately became motionless in a crouched position with fluffed plumage; the only noticeable movement was the flashing white of its eyelid. The fledgling yawned twice and tucked its beak over its shoulder and under its scapulars at 20:15. It aroused at 20:30 but settled to sleep again with beak tucked under its scapulars 4 min later. It remained motionless until it was too dark for further observation (20:46). The fledgling was still present in the roost at 04:00 (twilight) the next morning but had departed by 04:30.

The roost site used by the fledgling dipper was a branch in a small cluster of cottonwood leaves 1.5 m from the trunk of a 7.5 m tall cottonwood (diameter breast height = 17 cm) and about 1.5 m above a small rapid in the creek. The site appeared to be well protected from potential predator attack. The roost was near the tip of a small (ca 2 cm diameter) flexible branch that would have vibrated if any predator used it to approach the sleeping dipper, and the roosting bird overhung fast moving water, thereby restricting predators to approach from the air or along the branch. Finally, a small cluster of cottonwood leaves partially hid the fledgling from the sides and overhead, presumably making visual detection by a predator less probable. The roost was less protected from unfavorable weather, such as wind-driven precipitation.

Potential roost sites similar to that used by the fledgling dipper appear to be numerous along many streams where dippers are present in western Montana (pers. obs.). Furthermore, cottonwood, willow (*Salix* spp.), birch (*Betula* spp.), alder (*Alnus* spp.) and dogwood (*Cornus* spp.) are regular components of riparian corridors in mountain foothills of western North America (Bakus 1959, Price and Bock 1983, Knight 1994). Use of nocturnal roosts in trees and shrubs overhanging moving water could be a more prevalent behavior among American Dippers than previously suspected, particularly among fledglings and juveniles where predation is potentially great.

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Perch Proximity Correlates with Higher Rates of Cowbird Parasitism of Ground Nesting Song Sparrows

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ABSTRACT.—The reproductive success of avian brood parasites depends, to a great extent, on their ability to locate host nests that are at the appropriate stages of the host laying cycle. Consequently, brood parasites are expected to possess elaborate mechanisms and search modes to locate potential host nests. Through observing a population of Song Sparrows (*Melospiza melodia*) parasitized by the Brown-headed Cowbird (*Molothrus ater*) we examined two specific factors that may influence cowbird parasitism of a ground nesting host. Proximity to potential perches was a significant predictor of cowbird parasitism, but overhead nest visibility, either classified dichotomously as visible or not, or measured as the absolute area of a nest visible to an observer, was not correlated with the likelihood of parasitism. Comparisons with previous studies suggest that female cowbirds use similar nest searching mechanisms in open habitats, irrespective of the height of host nests. *Received 16 April 1999, accepted 23 Aug. 1999.*

The reproductive success of avian brood parasites and their effect on host populations depend, to a great extent, on the number of potential host nests and the stage at which host nests are located (Payne 1977, Rothstein 1990). Consequently, there has been considerable effort to determine the cues and search modes that brood parasites use to find nests (Lowther 1979, Thompson and Gottfried 1981, Yahner and DeLong 1992, Vogl et al. 1997, Clotfelter 1998, Teuschl et al. 1998).

The Brown-headed Cowbird (*Molothrus ater*) is a generalist brood parasite known to parasitize more than 220 bird species (Friedmann 1963, Lowther 1993). There is behavioral evidence (Fleischer 1985; but see McGeen and McGeen 1968) and genetic evidence (Alderson et al 1999, Gibbs et al. 1997) that individual female cowbirds may lay eggs in nests of more than one host species. Because the many host species of the Brown-headed Cowbird also build nests at different heights and on many substrates (Lowther 1993, Martin 1993), the mechanisms by which cowbirds find these nests are particularly intriguing.

There are at least four non-exclusive hypotheses proposed to explain the mechanisms and cues used for nest finding by Brown-headed Cowbirds (Lowther 1993, Clotfelter 1998). (1) The nest exposure hypothesis suggests that the more visible the nest of a potential host is, the more likely it is to be parasitized (Martin 1993). (2) The perch proximity hypothesis proposes that female cowbirds are better able to locate host nests when they can observe them from above at a nearby perch (Alvarez 1993, Paton 1994, Romig and Crawford 1995, Clotfelter 1998, Larison et al. 1998). (3) The nesting cue hypothesis asserts that the intensity of host nest defense correlates positively with the proximity of the parasite to the host nest and, thus, the escalation of defensive behavior may serve as a cue for the searching parasite (Smith 1981, Smith et al. 1984, Uyehara and Narins 1995; but see Gill et al.

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1997). (4) Finally, the host activity hypothesis suggests that vocal and visible activities of hosts associated with territoriality, nest building, and egg laying may attract brood parasites and consequently increase the likelihood of parasitism (Uyehara and Narins 1995, Clotfelter 1998).

Here we report on two specific factors that may relate to the parasitism of ground nesting Song Sparrows (*Melospiza melodia*) by Brown-headed Cowbirds: overhead visibility and distance to potential perches.

METHODS

We studied Song Sparrows and Brown-headed Cowbirds near both units of the Cornell Experimental Ponds in Ithaca, New York in 1998 and 1999 (about 1.5 km^2, for site description see Hauber 1998). Between April and June 1998 using walk-in traps we trapped and banded 18 female cowbirds in the area, 4 of which were recaptured between April and June 1999 at the same traps. We estimated 30 active Song Sparrow territories (indicated by censuses of singing males and counts of simultaneously active nests) within the fenced boundaries of these sites each year. Song Sparrows breed in Ithaca from early May until mid-July, and they nest along the banks of the ponds and in the surrounding fields mostly on the ground.

The location of each sparrow nest was marked with small pieces of flagging tape about 1 m north and south of the nest. All nests that were depredated during the laying period were excluded from the analyses because we did not know whether these nests had been parasitized. Because we did not observe Song Sparrows reject cowbird, House Sparrow (*Passer domesticus*), or plastic eggs at our study site (Hauber, unpub. data), and because no nests were abandoned upon parasitism (Hauber, in press), we assumed that nests found without cowbird eggs or chicks had not been parasitized.

We found 6 nests during the nest building and laying stages in 1998 and 2 (33%) of these were subsequently parasitized. This proportion was similar to the rate of parasitism of nests found after clutch completion [5 (26%) of 19; Fisher's Exact test; $P > 0.05$] in the same year. Therefore, we do not believe that flagging the nests biased nest discovery by parasites and we included ground nests found both before and after egg laying in our analyses. We monitored nest contents every 24–48 hours between 1 May and 8 June 1998 and 1 May and 31 May 1999. For a different study, we regularly trapped and housed several female cowbirds overnight after these periods, therefore we did not include any later nests in the analyses.

To study nest visibility, we photographed most nests upon discovery with a digital camera (Philips ESP 2/17, picture setting N) from a tripod 0.5 m directly above each nest (1998: $n = 20$, 1999: $n = 3$). We transferred the pictures into a Power Macintosh and classified each nest as either visible (i.e., part of the nest structure can be seen on the image despite vegetation) or not. We also traced the outlines of the visible portion of each sparrow nest in the photographs and calculated its absolute visible area using NIH Image 1.61 (U.S. National Institutes of Health 1999).

To quantify distance from potential perches, we measured the horizontal distance from the center of each nest found in 1998 to the base of (1) the nearest woody vegetation or permanent object (e.g., fence, nest-box pole) of any height, (2) the nearest woody vegetation or object at least 2 m tall, and (3) the nearest woody vegetation or object at least 3 m tall. We chose these heights to follow the methodology of Clotfelter (1998). Because of the small sample sizes and non-normality of data, we used the non-parametric Fisher's Exact and Mann-Whitney tests in Statview 5.0 (SAS Institute, Inc.) to analyze our data. All values are reported as mean ± standard deviation.

RESULTS

We found 28 active Song Sparrow nests on the ground at the various stages of the building and laying (9 of 28 nests, 32%), incubating (15 nests, 54%), and nestling (4 nests, 14%) periods, of which 9 nests (32%) were parasitized by cowbirds. Three parasitized nests (33%) had two cowbird eggs and all others had single cowbird eggs.

There was no significant difference between the proportions of visible parasitized nests and visible unparasitized nests (3 visible nests of 7 parasitized nests and 7 visible nests of 16 unparasitized nests; Fisher's Exact test: $P > 0.05$). Neither did the absolute areas visible from directly above each nest differ between parasitized (9.8 ± 16 cm^2, $n = 7$) and unparasitized nests (8.8 ± 17 cm^2, $n = 16$; Mann-Whitney test: $U = 53$, $P > 0.05$).

Parasitized nests in 1998 ($n = 7$) were no closer or more distant from the nearest woody vegetation or permanent object than unparasitized nests ($n = 18$; Mann-Whitney test; $U = 44$, $P > 0.05$; Fig. 1). However, parasitized sparrow nests ($n = 7$) were significantly closer than unparasitized nests ($n = 18$) to trees and permanent objects of at least 2 m height (Mann-Whitney test: $U = 28$, $P < 0.034$) and of at least 3 m height (Mann-Whitney test: $U = 24$, $P < 0.018$; Fig. 1). When restricting analyses to nests with hatchlings, parasitized nests ($n = 5$) still tended to be closer to objects of at least 2 and 3 m height (distances: 3.0 ± 3.2 m and 8.1 ± 6.5 m, respectively) than unparasitized nests ($n = 14$, distances: 14

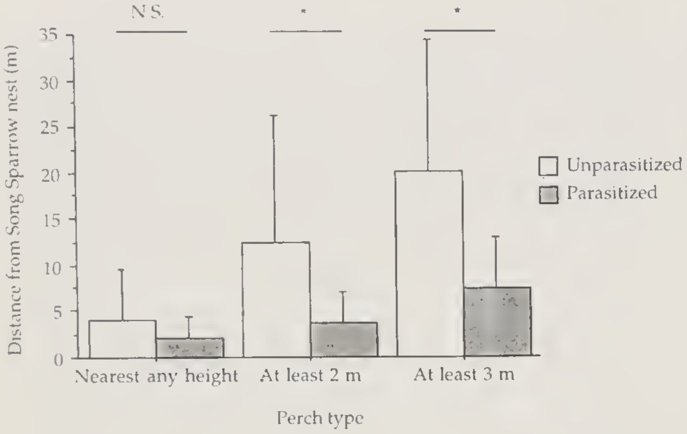

FIG. 1. Comparison of mean distances (+ SD) from parasitized (n = 7) and unparasitized (n = 18) Song Sparrow nests to the nearest potential perches of any height, and perches at least 2 m and 3 m tall (Mann-Whitney tests: N.S.: $P > 0.05$, *: $P < 0.05$).

± 15 m and 22 ± 15 m, respectively; Mann-Whitney tests: $U = 12$, $P < 0.033$ and $U = 15$, $P < 0.064$, respectively).

DISCUSSION

We tested the predictions of two hypotheses to describe the cues and search modes used by brood parasitic Brown-headed Cowbirds to locate host nests. In contrast to the prediction of the nest exposure hypothesis, we found that overhead nest visibility was not correlated with parasitism of ground nesting Song Sparrows. In support of the perch proximity hypothesis, the mean distances of sparrow nests to the nearest potential perches at least 2 or 3 m tall were significantly closer for parasitized nests.

Previous research on Song Sparrows and Brown-headed Cowbirds showed indirect support for the perch proximity and nest visibility hypotheses (Larison et al. 1998); nests in environments with denser foliage between 2 and 3 m heights (i.e., rich in potential perches) were more likely to be parasitized and nests with denser foliage cover below 1 m (i.e., more limited nest visibility) were less likely to be parasitized.

Recently, Clotfelter (1998) tested several nest searching hypotheses for cowbirds that parasitized open-field nesting Red-winged Blackbirds (*Agelaius phoeniceus*). He found that perch proximity, but not nest exposure, was positively correlated with the likelihood of being parasitized. Using similar methodologies, we found that ground nesting Song Sparrows showed similar relationships. It is possible that in open habitats female cowbirds use a general sit-and-watch search mode (Smith 1981), regardless of whether the potential host nests are on the ground or above it.

That female cowbirds use high perches for a sit-and-watch strategy in the territories of host species to locate potential host nests has been frequently documented anecdotally (Lowther 1993). In agreement with these observations we found that proximity to tall perches was a significant predictor of cowbird parasitism of ground nesting Song Sparrows. However, we found that overhead nest visibility was not correlated with the likelihood of parasitism. This suggests that female cowbirds may not be locating host nests from these perches by spotting the more exposed nests, instead other factors, such as host activity, may also be important predictors of cowbird parasitism (Clotfelter 1998).

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Male Dickcissels Feed Nestlings in East-central Illinois

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ABSTRACT.—We observed male Dickcissels (*Spiza americana*) commonly feeding nestlings in Conservation Reserve Program (CRP) fields in 1997 in east-central Illinois. Male Dickcissels fed nestlings at six of the eight nests we observed, accounting for 37% of the total nest visits. Overall, females made significantly more nest visits than males. However, at the six male-assisted nests, the number of male and female nest visits did not differ significantly. Male Dickcissel feeding behavior may have been prompted by low food abundance. Males were not observed feeding nestlings in 1998, when overall nest success was higher and nestling starvation was less than in 1997. *Received 29 March 1999, accepted 15 Sept. 1999.*

Nearly all male passerines feed their nestlings (Kendeigh 1952, Verner and Willson 1966, Silver et al. 1985). Among North American species, only males of the Dickcissel (*Spiza americana*) and the Boat-tailed Grackle (*Quiscalus major*) do not provide their nestlings with food (Verner and Willson 1969).

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We found reports from only two nests at which male Dickcissels fed nestlings (Purdie 1878, Bellrose 1936). Purdie (1878) observed one male feeding nestlings in Massachusetts and Bellrose (1936) reported a rather ambiguous sighting of two Dickcissels feeding nestlings in northern Illinois during late August. No other study has documented significant male assistance in the Dickcissel (Gross 1921, Crabb 1923, Zimmerman 1966, Schartz and Zimmerman 1971, Fretwell 1977, Fink 1984). Nonetheless, we observed male Dickcissels commonly feeding nestlings at our study sites in east-central Illinois in 1997. The objective of our study was to determine the extent of this male assistance.

STUDY AREA AND METHODS

Our research was conducted from 26 June to 22 July 1997 in Conservation Reserve Program (CRP) fields of Coles and Cumberland counties, Illinois. We located all Dickcissel nests and checked them every 2–3 days to determine their fate. One to four 60 min observations were made at each Dickcissel nest containing nestlings with a 20× spotting scope from at least 50 m away. Each time an adult Dickcissel was observed visiting a nest, we recorded the sex of the individual and whether the individual was carrying food. Prior to most nest visits, adult Dickcissels would perch near the nest for a few seconds enabling us to determine if the individual was carrying food. In these cases, individuals were always seen carrying food to the nest. Males and females exhibited this behavior during 82% (61 of 74) and 56% (72 of 128) of the nest visits, respectively. In the absence of this perching behavior we frequently were unable to see individuals clearly enough to determine if they were carrying food. Given the strong evidence that food delivery nearly always accompanied nest visits, we included all nest visits in our analyses. Paired t-tests were used to compare the number of nest visits by males and females (Wilkinson 1997).

RESULTS

A total of 202 nest visits were observed at eight nests (Table 1). Male Dickcissels visited six of the eight nests (75%), accounting for 37% (74) of the total nest visits. At the six male-assisted nests, males made 42% of the feeding trips. Overall, females made significantly more nest visits (128) than males (74; $t = 2.6$, df = 7, $P < 0.05$). At male-assisted nests, males made as many nests visits as females did ($t = 1.8$, df = 5, $P > 0.05$). Prior to (and prompting) our data collection at these eight nests, at least two other males were observed feeding their nestlings.

TABLE 1. Number of female and male nest visits for each of eight Dickcissel nests in east-central Illinois.

Nest #	Number of nest visits: Female	Number of nest visits: Male	% Nest visits by male
1	19	19	50
2	19	9	32
3	8	8	50
4	24	21	47
5	10	10	50
6	23	7	23
7	18	0	0
8	7	0	0
Total	128	74	37
Male visited nests	103	74	42

DISCUSSION

These results represent the first reported occurrence of substantial male parental care in Dickcissels. Male Dickcissel assistance at the nest, though rare, may be an adaptive behavior that might emerge under specific environmental conditions. The advantages of male parental care are often significant (see Bart and Tornes 1989, Wolf et al. 1988, Dunn and Hannon 1989). However, males may be more inclined to provide (additional) parental care during unfavorable environmental conditions when a significant increase in fitness can be obtained (Emlen and Oring 1977, Oring 1982). Several failed nests in our study area were attributed to starvation, implying that 1997 was a difficult year in east-central Illinois for Dickcissels (E. K. Bollinger, unpubl. data) and other grassland birds (Davison 1998). We did not quantify food abundance in 1997. However, all eight Dickcissel nests found in the same fields in the following year (1998) successfully fledged at least one nestling, but not a single male Dickcissel was observed visiting a nest (E. K. Bollinger, unpubl. data). In 1997, 7 of 63 nestlings (11%, all nests combined) were found dead in the nest (probably as a result of starvation), whereas no nestlings were found dead in the nest in 1998 (26 nestlings). These data further support the view that male parental care in many birds may be phenotypically plastic, present during certain years (Emlen and Oring 1977, Oring 1982) but relatively unimportant and often absent when food resources are more abundant (Dunn and Hannon 1992).

The occurrence of male parental care in Red-winged Blackbirds (*Agelaius phoeniceus*) is geographically variable (reviewed in Beletsky and Orians 1990). Males consistently provide their nestlings with food in some populations but not in others (Beletsky and Orians 1990). It is possible that parental care is geographically variable in Dickcissels and additional studies may reveal other populations with male assistance; however, this seems unlikely given that the Dickcissel has been studied throughout its breeding range. In addition, our population of Dickcissels exhibited male parental care one year (1997) but not the next (1998), further supporting the hypothesis that male Dickcissels fed nestlings in 1997 to offset limited food resources.

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Wilson Bull., 112(1), 2000, pp. 156–161

Ornithological Literature

Edited by Sara R. Morris

THE BIRD ALMANAC: THE ULTIMATE GUIDE TO ESSENTIAL FACTS AND FIGURES OF THE WORLD'S BIRDS. By David M. Bird. Firefly Books, Buffalo, New York. 1999: 460 pp., 17 unnumbered black and white illustrations, numerous unnumbered tables. $19.95 (paper), $65.00 (cloth).—In a single volume, David Bird has compiled many of the facts and figures about birds and provided resources for those who study birds. The book is divided into sections that will be useful to professional ornithologists, including anatomy, physiology, reproduction, mortality, threatened and endangered species, resources for professional ornithologists, and a world checklist of birds. Additional sections will have appeal to bird enthusiasts, including American and British equivalencies for names of birds, mascot birds, bird-watching, attracting birds to the backyard, who's who in ornithology and conservation, resources for bird lovers, and record holders. Each section has a surprising amount of information. For example, the section on reproduction includes tables of territory sizes, song repertoire sizes, time of initiation of singing, number of sperm storage tubules, duration of sperm storage, clutch size, incubation period, incubation times, and sex ratios; descriptions of nest types and patterns of development; and illustrations of gametes, eggs, and embryonic development. Anyone teaching classes about birds will have a variety of interesting facts and useful illustrations to use in the classroom. Bird has included extensive citations for the information he presents, allowing anyone interested in learning more about a particular topic to read the original source for additional details.

The resources included in the book for bird watchers and ornithologists are equally impressive. Bird has compiled traditional resources like contact information for bird-related societies, contact information for scientific journals and bird magazines, addresses for bird banding organizations, rare bird alert numbers (and web addresses), annotated lists of CD-ROMs and software, and lists of bird videos and sound recordings. Ornithologists will find contact information for sources of optical equipment, sound-recording equipment, telemetry gear, banding supplies and equipment, organizations that provide DNA sexing, and specialized video equipment. There are also extensive on-line references like internet links to world-wide birding web sites, addresses of bird-watching and ornithological discussion groups, and subscription information for bird related e-mail lists.

As with any volume of this magnitude, there are inaccuracies and oversights. For example, the illustration of the bird skeleton has labeled the tarsometatarsus as the tarsus, and it does not label the sternum but does label the keel. In a number of the tables, only the common name is given, even when numerous species have the same general name (e.g., crow, blackbird, or magpie).

With the wealth of information packed into this book, it will provide a wonderful resource for both professionals and amateurs. Ornithologists and bird enthusiasts should both consider this book for their libraries.—SARA R. MORRIS.

ENDEMIC BIRD AREAS OF THE WORLD: PRIORITIES FOR BIODIVERSITY CONSERVATION. By Alison J. Stattersfield, Michael J. Crosby, Adrian J. Long, and David C. Wege. Bird Life International, Cambridge. 1998: 846 pp., 120 maps covering major areas of avian endemism and several hundred tabulations. $60.00 (paper).—This remarkable work documents, in great detail, all the major endemic bird areas of the world. Detailed maps show basic physiography and features. The species tabulations cover global status, where each rare species occurs, its altitudinal range, and details of habitat. Over 300 contributors combined to produce the data sets. There are several dozen habitat photos.

Each endemic bird area is individually explored with its geographic position, area, geographic and habitat features, history, current conservation status in terms of anthropogenic change, and threats to conservation discussed. The major bird species of each area are reviewed and discussed in the light of their ecology and status.

This book represents a remarkable reference. Details are complete and precise. As one flips from one fascinating part of the natural world to another, it is hard to put the book down. The book succeeds admirably in its message of providing a definitive documentation of the status of the world's birds and warnings as to their future.

Introductory sections discuss such general issues as Biodiversity and its loss, how the EBAs were identified and explored, the relationship between bird species richness and geographic area, and the distribution of restricted range species in the different countries. A prioritization scheme for conservation is detailed, as is the conservation relevance of each EBA. Reference is made as to how patterns of endemism in birds compare to other groups.

There is so much fascinating and important information in this volume that it is difficult to select one for comment at the expense of another. With interests in the southeast area, I found that being provided with a detailed and updated account of the avifauna of the different islands particularly rewarding. Information from all parts of the world is equally good. In recent years there have been major attempts to ornithologically re-explore islands not visited since the earliest bird collectors. Learning the results of this effort is fascinating. The book has documentation in the interests of conservation as its major objective. However, every vertebrate ecologist and biogeographer will find the work fascinating.

I highly recommend that anybody interested in birds obtain a copy of this book.—ALLEN KEAST.

THE ERA OF ALLAN R. PHILLIPS: A FESTSCHRIFT. Compiled by Robert W. Dickerman. Horizon Communications, Albuquerque, New Mexico. 1997: 246 pp., 5 color plates, 12 black and white photos, 32 tables, and 21 figures. No price given. (cloth).—This book honors the life and accomplishments of Allan R. Phillips (1914–1996), a prominent taxonomist and collector who for over six decades actively studied North American birds, particularly those of the southwestern United States and Mexico. The volume is introduced by two papers dealing with Phillips' life, character, and personality by two of Phillips' close professional associates; an affectionate biography prepared by Bob Dickerman, the compiler, and a long essay by John Hubbard. In the same vein, Roy Johnson reviewed ARP's specific contributions to Arizona ornithology. Phillips emerges as a study in high contrasts—at once a brilliant, indefatigable colleague and mentor with exhaustive knowledge of the birds and literature in the regions where he worked but at the same time a person knotted with so many complexes that irascibility, abrasiveness, and paranoia came to be the features that defined his interactions with a significant number of America's ornithologists. I remember him mostly from the latter perspective.

Whatever his mixed set of descriptors might be, Allan Phillips was easily one of the century's most unswerving advocates of specimen-related ornithology, and this volume appropriately reflects these interests. Thus, original investigations of geographic variation, taxonomy, and distribution of selected species form the core of this Festschrift. These include papers on the Flammulated Owl (*Otus flammeolus*) by Marshall, Spotted Owl (*Strix occidentalis*) by Dickerman, Downy Woodpecker (*Picoides pubescens*) by Browning, Scaly-throated Foliage-Gleaner (*Anabacerthia variegaticeps*) by Winker, Brown Creeper (*Certhia americana*) by Unitt and Rea, and Northern Cardinal (*Cardinalis cardinalis*) by Parkes. One paleontologic paper is included, Rea's description of a new species of Late Pleistocene parrot (*Rhynchopsitta phillipsi*) from cave material in southern Nuevo Leon, Mexico. Webster offers an analysis of skeletal features that form the basis for a key to the genera of New World warblers. In an especially thought-provoking paper on the Clapper Rail (*Rallus longirostris*) and King Rail (*Rallus elegans*) complex, Olson argues persuasively for their species status, despite hybridization and phenotypic near-identity, and for the transfer of Pacific Coastal Californian, Baja Californian, and central and western Mexican populations from the Clapper Rail, where they are currently included, to status as subspecies of the King Rail. (A broadscale genetic treatment of all populations of these rails could provide the data for a fascinating doctoral thesis.) In keeping with the collection-related theme of the book, two papers discuss specimen identification of species in difficult genera (*Empidonax* and *Contopus*; Pyle) and (*Catharus*; Patten) and another contribution by Pyle et al. offers new data on timing of molt and age criteria in North American hummingbirds. A brief nomenclatural paper by Banks unravels the complexities surrounding determination of the correct binomial for Lawrence's Flycatcher (*Lathrotriccus flaviventris*). Finally, in a paper assembled by Hubbard from partial manuscripts, Phillips discusses the problem of accurately tallying the numbers of species and subspecies of Recent birds. As a splitter, he concluded, unsurprisingly, that estimates presented by others are overly conservative.

Additional papers are clearly ecological in approach. In this category would fall the well-documented study by Ouellet on geographic variation in comparative foraging in the Downy Woodpecker and Hairy Woodpecker (*P. villosus*). Two papers in Spanish, centered in El Valle de Cuatrocienegas, Coahuila, Mexico, described the summer and autumn avifaunas of creosotebush desert (by Garcia-Salas et al.) and the breeding avifauna of mesquite-acacia shrubland (by Gonzales-Rojas et al.). With accompanying eye-popping photos, Monson noted the occurrence in 1963 of a flock of millions of Dickcissels (*Spiza americana*) in Sinaloa, Mexico, perhaps "the first and only time that probably the entire species migrated up the Pacific coast."

The book ends with (1) a list of the names and references of the nine subspecies and three species named in Phillips' honor; (2) an annotated list prepared by Dickerman and Parkes of the names, references, type localities, and, where known, the catalogue numbers and disposition of type specimen material for the 131 taxa described by Phillips; and (3) a list prepared by Hubbard et al. of Phillips' 172 publications (1933–1997). This material will be exceptionally useful to avian taxonomists and geographers generally.

The book received minimal editing. Thus, in my review copy, the text only makes sense if one connects the words at the bottom of page one with those at the top of page 3 and if one connects the bottom of page 2 with the top of page 5 (page 4 is a photo). A page of "Corregida" corrects errors discovered on other pages as of 15 June 1997. The casual editing also allowed authors occasionally to indulge in off-the-wall ramblings (see Marshall's hysterical account of how one European buffoon maligned the taxonomy of New World *Otus*).

My copy of the Festschrift is attractively bound and should withstand regular use. The narrow margins and lack of an index are trivial weaknesses.

Overall, the contributions of this Festschrift form a solid body of new information worthy of close attention. Furthermore, *en masse* they implicitly convey the inescapable truth that collections of birds anchor ornithology both to science and to reality. The volume will be a valuable reference for anyone working in New World avian systematics and distribution, and several sections will be required reading for ornithological historians. The compiler and authors deserve appreciation for their efforts.—NED K. JOHNSON.

THE LIFE OF BIRDS. By David Attenborough. Princeton University Press, Princeton, New Jersey. 1998: 320 pp., numerous unnumbered photographs. $29.95 (cloth).—This book is based on the ten-part PBS program hosted by the author, David Attenborough. The chapters, corresponding to topics covered in the series, are "To Fly or Not to Fly," "The Mastery of Flight," "The Insatiable Appetite," "Meat-eaters," "Fishing for a Living," "Signals and Songs," "Finding Partners," "The Demands of the Egg," "The Problems of Parenthood," and "The Limits of Endurance." Each chapter is easy to read and includes interesting anecdotes that will hook readers into that particular topic. For example, in the first chapter, the author discusses many groups of birds that are now flightless. In addition to discussing specific examples of species that have evolved flightlessness in the absence of predators, Attenborough also details an encounter one might have with a kiwi on a beach on an island in southern New Zealand, such that one can almost see and hear the kiwi on the beach.

Well-read ornithologists and bird watchers may be disappointed with the level of detail in the book. Given the scope of the work and the number of topics covered, there is no way to adequately cover all the topics in a single volume. Most topics could fill an entire volume individually. Attenborough also covers additional aspects of avian biology in each chapter. Avian senses are covered in a variety of chapters including "To Fly or Not to Fly" and "Meat-eaters." Regardless, readers may wonder at the choice of topics and the areas of concentration in the book. For example, devoting three chapters to feeding ("The Insatiable Appetite," "Meat-eaters," and "Fishing for a Living") seems excessive, particularly given a single chapter covering adaptations for flight, different types of flight, migration, and navigation.

The photographs included in this book are absolutely stunning and alone would be well worth the cost of the book. Images are well chosen to illustrate points and include species from all over the world. The chapter on finding partners includes a Blue-footed Booby (*Sula nebouxii*) showing off his feet, ritual courtship feeding by terns, aerial displays of harriers, dancing by cranes, grebe presentations and displays, egret plumes, bird of paradise displays, and bowerbird bowers. The chapter on fishing includes a variety of interesting photographs, including kingfishers, a dipper, an anhinga, penguins, and pelicans underwater as well as a truly phenomenal photograph of a booby diving. My only criticism of the illustrations is that I would have preferred more detailed descriptions of the photographs than the few words provided. Many of the photographs do not give the full common name or a location of the picture.

As an ornithologist, I was disappointed with common names in all lower case letters and with a lack of scientific names. Likewise, terms like *Archaeopteryx* are not italicized and may lead to a perpetuation of sloppy writing by readers who have not been trained classically. The conventions of capitalizing standardized common names and including scientific names are extremely useful when trying to find more information about a species covered in a book. Nonetheless, the book is extremely easy to read, contains interesting information to inform or remind the reader of the amazing lives of birds, and is beautifully illustrated. This book is highly recommended for any bird enthusiast.—SARA R. MORRIS.

BULL'S BIRDS OF NEW YORK STATE. Edited by Emanuel Levine. Cornell University Press, Ithaca, New York. 1998: 622 pp., numerous unnumbered black and white illustrations, seven maps. $39.95 (cloth).—This updated version of the classic volume on the birds of New York is a must for anyone interested in the state's avifauna. Initial sections about the natural history of New York State and bird biology are followed by species accounts for the 451 species that have been recorded on the New York State checklist.

The introductory section includes an explanation of the layout of the book and definitions of terms used in each section. Following the explanation of the structure of the book are a series of essays that cover topics related to the avifauna of New York, including the physical environment, bird habitats, the role of the Federation of New York State Bird Clubs in conservation, long-term changes in New York's birdlife, and a discussion of taxonomy. The introduction is concluded with a checklist of the birds of New York State. In addition to a list of species and their breeding status, this section also includes detailed notes on how species were added to or deleted from earlier editions of the state checklist.

Individual species accounts were written by authors familiar with the species in New York. The species accounts follow the sixth edition of *The AOU Check-list of North American Birds* (1983). Taxonomic changes in the seventh edition are detailed in a section prior to the checklist and species accounts. Each account includes the range of the species; its status in New York (including abundance); location and timing of its occurrence in the state, separated into breeding and nonbreeding seasons for species known to breed in the state; and additional remarks if appropriate. Ranges include the entire known range of the species, not simply the range in New York state. Additional information included in some accounts are the extreme dates of occurrence and the maximum number of individuals seen. These accounts also include references that are listed in an extensive bibliography. Most accounts are limited to a single page; however, a number of species of special interest or concern have more extensive accounts, including the Peregrine Falcon (*Falco peregrinus*), the Common Tern (*Sterna hirundo*), and the Golden-winged Warbler (*Vermivora chrysoptera*).

Bull's Birds of New York State is undoubtedly the best reference on the avifauna in the state. The effort and detail that went into preparing the species accounts is clearly evident. This volume is highly recommended for birders and ornithologists interested in the birdlife of New York State.—SARA R. MORRIS.

RAPTOR MIGRATION WATCH-SITE MANUAL. By Keith L. Bildstein and Jorje I. Zalles, Editors. Available in English or Spanish from Hawks Aloft Worldwide, Hawk Mountain Sanctuary Association, R.R. 2 Box 191, Kempton, Pennsylvania 19529 USA. 1995: vi + 177 pp., 1 numbered text figure, 2 illustrations, 19 appendix tables. $20.00 (paper)—For more than half a century, Hawk Mountain Sanctuary has led the way in popularizing, monitoring, and protecting hawks, eagles, and falcons in eastern North America. Recognizing that migratory raptors are in need of protection worldwide, Hawk Mountain Sanctuary broadened its efforts in 1988 by establishing a global conservation initiative called Hawks Aloft Worldwide. This publication represents the culmination of 60 years of raptor conservation at Hawk Mountain Sanctuary, along with the combined talents of a number of other raptor biologists from both North and South America.

As indicated by the title, this volume contains information applicable to raptor conservationists around the world. Organized topically, 13 chapters include "Raptor Migration and Conservation Biology," "Investigating Raptor Migration Biology and Ecology," "Monitoring the Abundance and Distribution of Migrating Raptors," "Managing Data," "Environmental Education," "Ecotourism," "Membership Programs," "Volunteer Resources," "The Watch-site and Agenda 21 (from the Earth Summit, Brazil, 1992)," "Watch-site Diagnostic," "A Bibliography of Latin American Raptors," and "Case Studies." Collectively, these chapters provide a blueprint for an integrated approach to raptor conservation throughout the western hemisphere.

An introductory chapter lays the groundwork for the remainder of the text by first providing a succinct history of Hawk Mountain Sanctuary, followed by a segue that explains how the Hawk Mountain experience can be used as a model for establishing community-based raptor conservation elsewhere in the world. The next several chapters focus on aspects of raptor migration biology and elements essential to establishing an effective monitoring program for migrant raptors. The importance of data management is well summarized, and the value of integrating hawk migration data with other long-term databases (e.g., Breeding Bird Census, Christmas Bird Count) is properly emphasized.

Two of the most significant sections of this manual are devoted to environmental education and ecotourism—both essential elements of any effective raptor monitoring program. A thoughtful consideration of the elements described for a watch-site environmental education program will help readers appreciate the wisdom in the words of Hawk Mountain Sanctuary's first curator, Maurice Broun: "I like to think of the Sanctuary as a 'school in the clouds,' where one sees and learns about nature by association, in an effortless manner; where knowledge of nature is tempered with humor, kindled by good fellowship, sparked by the inspiration of many inquiring minds and kindred spirits." Indeed, the model provided by the River of Raptors program at Vera Cruz, Mexico, stands as an example how science can be effectively integrated with education and ecotourism.

The closing chapters describe how membership programs and volunteerism are important to maintaining an effective, long-term watch-site effort. The rationale for maintaining such programs is given even treatment and appropriate caveats are provided about the potential pitfalls of such efforts. An especially creative section describes the potential for coordinating a watch-site's program with the goals of Agenda 21 in creating sustainable development activities. The manual ends with a useful watch-site diagnostic template that provides specific guidance for individuals and organizations interested in setting up a long-term watch-site program. The diagnostic can be particularly useful in guiding strategic planning and feasibility analyses.

Seven Latin American case studies described in the final chapter provide testimony to the value of establishing long-term monitoring watch-sites, as well as how these sites are making significant contributions to the conservation of raptors and the overall understanding of raptor biology. These case study briefs, along with the extensive bibliographies provided at the end of each of the well-crafted "working" chapters, make this manual a valuable contribution to the raptor conservation literature, as well as conservation biology in general. Once again, Hawk Mountain Sanctuary has set a high standard for other groups to follow. This manual should be required reading for anyone with an interest in raptor conservation, and its availability in Spanish should make it particularly useful to those involved with long-term monitoring efforts in Latin America.—WAYNE R. PETERSEN.

THE BIRDS OF PENINSULAR MALAYSIA. By Derek Holmes, illus. by Karen Phillips. Oxford University Press, Kuala Lumpur, New York, Oxford. 1998: 96 pp., color plates, with about 160 species illustrated and 30 black-and-white marginal figures. $43.00 (cloth).—This delightful small book, beautifully illustrated and sufficiently small and light to be readily carried, covers the common Malaysian birds that any tourist bird-watcher may encounter. The figures are large and lifelike. The short text gives a brief description of each species, measurements, and notes on its habitat and call notes. Attention is drawn to species with which it may be confused. Appendices at the end provide a supplementary list of the Borneo endemics not covered in the text and a list of Malay names. There is a species index.

Derek Holmes, the author, is a long term resident and expert on the birds of Malaysia, Indonesia, Sumatra, and Kalimantan. The illustrator, Karen Phillips, is the best available in that part of the world. Glancing at the plates makes one wish to depart immediately for Malaysia. This book will be a boon. It is highly recommended.—ALLEN KEAST.

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XXIII International Ornithological Congress Beijing, China, August 2002

Scientific Program

The XXIII International Ornithological Congress will be held in Beijing, China, on 11–17 August 2002. The following officers were elected: Honorary President, Professor Ernst Sutter (Switzerland), President, Professor Walter Bock (U.S.A., e-mail <wb4@columbia.edu>), Vice President, Professor Jacques Blondel (France, e-mail <blondel@cefe.cnrs-mop.fr>), Secretary-General, Professor Xu Weishu (China, e-mail <s-g@ioc.org.cn>), Assistant Secretary-General, The Honorable Liu Feng (China, e-mail <liufeng@public.bta.net.cn>), Secretary of the International Ornithological Committee, Dr. Dominique G. Homberger (U.S.A., e-mail <zodhomb@lsu.edu>).

The Scientific Program Committee for the XXIII International Ornithological Congress has been appointed under the chairmanship of Dr. Fernando Spina (Istituto Nazionale per la Fauna Selvatica, Via Ca' Fornacetta 9, I-40064 Ozzano Emilia (BO), Italy. Phone: +39-051-65-12-111; Fax: +39-051-79-66-28; e-mail <infsioc@iperbole.bologna.it>) and includes the following members: Dr. Alexander V. Andreev (Russia, e-mail <ted@actor.ru>), Professor Ding Changqing (China, e-mail <dingcq@panda.ioz.ac.cn>), Professor Patricia Gowaty (U.S.A., e-mail <gowaty@ecology.uga.edu>), Professor Zheng Guangmei (China, e-mail <zhenggm@bnu.edu.cn>), Dr. Hiroyoshi Higuchi (Japan, e-mail <higuchi@uf.a.u-tokyo.ac.jp>), Dr. Lukas Jenni (Switzerland, e-mail <jennil@orninst.ch>), Professor Marek Konarzewski (Poland, e-mail <marekk@cksr.ac.bialystok.pl>), Dr. Theunis Piersma (The Netherlands, e-mail <theunis@nioz.nl>), Professor Pilai Poonswad (Thailand, e-mail <scpps@mucc.mahidol.ac.th>), Dr. Richard Schodde (Australia, e-mail <Richard.Schodde@dwe.csiro.au>), Dr. Lucia Liu Severinghaus (China, e-mail <zolls@gate.sinica.edu.tw>), Professor Hans Winkler (Austria, e-mail <H.Winkler@klivv.oeaw.ac.at>), Professor Zhang Zhengwang (China, e-mail <zzw@bnu.edu.cn>), in addition to the President, the Secretary-General and the Secretary.

General information on the congress can be obtained via e-mail <infocenter@ioc.org.cn>, or via the internet at <http://www.ioc.org.cn>. Information about the IOC can also be obtained from our new home page at <http://www.nmnh.si.edu/BIRDNET/IOC/>.

All inquiries about the scientific program of the 23rd congress, as well as comments and suggestions for the general program, plenary lectures, and symposia should be sent to Dr. Fernando Spina. The SPC will decide on the format and contents of the scientific program of the congress, which is expected to include Plenary Lectures, Symposia, Contributed papers (in the form of Oral presentations and Poster papers) and Round Table Discussions.

In previous congresses, the plenary speakers were internationally known ornithologists and chosen to cover a diversity of topics to ornithologists. Symposia contributions are intended for the general ornithologist rather than the specialist and should offer updated review papers on recent developments in a research field. Contributed papers provide a means for individual ornithologists to present their most recent findings and ideas to the congress. Round table discussions are workshops, discussion groups, etc. designed for exchange of ideas among specialists in a field. Round table discussions should not be used to present a longer lecture by the organizer of the discussion group or a series of symposium-type papers.

All interested ornithologists are invited and urged strongly to submit proposals for symposia and for plenary speakers. Proposals of plenary speakers should include the name and address (including e-mail address) of the proposed speaker, and a statement of the possible topic and why the person was proposed. Symposia proposals should include a title, a statement on the expected content of the symposium (not exceeding 1,800 characters), suggested symposia speakers (maximum 5, including postal and e-mail addresses), the suggested conveners (a primary convener and a co-convener, including their full postal and e-mail addresses). We strongly encourage use of the internet to submit proposals. The statements on symposia contents should preferably be sent as *.rtf format files. It is urged that contributors in each symposium be as international as possible. Round table discussions can also be proposed at this time although there will be a subsequent call for proposals for RTDs and for contributed papers.

Because BirdLife International has terminated its world-wide meetings just prior to the International Ornithological Congresses, and being the XXIII Congress the first ever held in Asia, the SPC is especially interested to solicit high standard proposals concerned with the contribution of Ornithology to biological conservation and wildlife management.

The SPC will meet in Beijing, China in mid-June 2000; hence all proposals should reach the Chair of the committee within the end of April 2000 at latest. Proposals can also be sent to individual members of the committee, but in this case submission should be earlier so that the proposal can be forwarded to the chair. We thank all interested ornithologists for their proposals and contribution to the scientific program of the Congress, and we look forward to a fruitful meeting in Beijing in the year 2002.

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THE WILSON BULLETIN

SUGGESTIONS TO AUTHORS

See Wilson Bulletin, 110:152–154, 1998 for more detailed “Instructions to Authors.”

http://www.urnmz.lsa.umich.edu/birds/wilsonbull.html

Submit four copies of manuscripts intended for publication in *The Wilson Bulletin,* neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Seventh Edition, 1998) insofar as scientific names of U.S., Canadian, Mexican, Central American, and West Indian birds are concerned. Abstracts should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the “CBE Scientific Style and Format Manual” (AIBS 1994). Photographs for illustrations should have good contrast and be on glossy paper. Submit prints unmounted and provide a brief but adequate legend for each figure with all captions on a single page. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

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If your address changes, notify the Society immediately. Send your complete new address to Ornithological Societies of North America, P.O. Box 1897, Lawrence, KS 66044-8897.

The permanent mailing address of the Wilson Ornithological Society is: ℅ The Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109. Persons having business with any of the officers may address them at their various addresses given on the back of the front cover, and all matters pertaining to the Bulletin should be sent directly to the Editor.

MEMBERSHIP INQUIRIES

Membership inquiries should be sent to Laurie J. Goodrich, Route 2 Box 301A, New Ringgold, PA 17960-9445; E-mail: goodrich@hawkmountain.org.

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THE WILSON ORNITHOLOGICAL SOCIETY

FOUNDED DECEMBER 3, 1888

Named after ALEXANDER WILSON, the first American Ornithologist.

Membership dues per calendar year are: Active, $21.00; Student, $15.00; Family, $25.00; Sustaining, $30.00; Life memberships $500 (payable in four installments).

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NEW SPECIES AND RECORDS OF BIRDS FROM PREHISTORIC SITES ON NIUE, SOUTHWEST PACIFIC

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ABSTRACT.—We report the first prehistoric bird bones from the isolated limestone island of Niue, South Pacific. Discovered in a cave known as Anakuli, the bones are Holocene in age but lack cultural association. They represent three extinct species: a night-heron (*Nycticorax kalavikai*), a new species known thus far only from Niue but closely related to an extinct undescribed species from Tonga; the "Niuafo'ou" Megapode (*Megapodius pritchardii*), known historically only from Niuafo'ou (Tonga) but recorded from prehistoric sites elsewhere in Tonga; and *Gallirallus huiatua*, a new species of flightless rail presumably endemic to Niue and distinct from extinct, flightless congeneric species from island groups immediately east (Cook Islands) and west (Tonga) of Niue. The first two species are in accord with the overall biogeographic affinity of the extant avifauna of Niue, which is West Polynesian rather than East Polynesian. *Received 15 Sept. 1999, accepted 15 Feb. 2000.*

The limestone island of Niue is isolated between the Cook Islands (800 km to the east), Samoa (560 km to the north-northwest), and Tonga (480 km to the west; Fig. 1). A large island by Polynesian standards (259 km^2), Niue attains a maximum elevation of 68 m in the perimeter ring of coralline limestone that surrounds a gently depressed (min elev. 34 m) central basin (Dept. Lands Survey New Zealand 1977). The geology of Niue, an uplifted Pliocene atoll, has been well described by Aharon and coworkers (1987), Wheeler and Aharon (1991), and Paulay and Spencer (1992).

The affinities of the indigenous terrestrial flora and fauna of Niue are West Polynesian (especially Tongan) rather than East Polynesian (Sykes 1970, Wodzicki 1971, Steadman 1997). The modern Niuean landbird fauna comprises 10 species (Townsend and Wetmore 1919, Wodzicki 1971, Kinsky and Yaldwyn 1981, Hay and Powlesland 1998, Powlesland and Hay 1998): three rails (*Porzana tabuensis samoensis, Gallirallus philippensis goodsoni, Porphyrio porphyrio* cf. *samoensis*), two columbids (*Ducula pacifica pacifica, Ptilinopus porphyraceus whitmeei**), a lorikeet (*Vini australis*), a barn-owl (*Tyto alba lulu*), a swiftlet (*Collocalia spodiopygia spodiopygia*), a triller (*Lalage maculosa whitmeei**), and a starling (*Aplonis tabuensis brunnescens**). The three subspecies endemic to Niue are marked with an asterisk (*). All 10 species are widespread in West Polynesia. Only *Porzana tabuensis* and *Ducula pacifica* occur on islands east of Niue.

Herein we document the former presence on Niue of three species of ground-dwelling birds, two of which are described as new herein.

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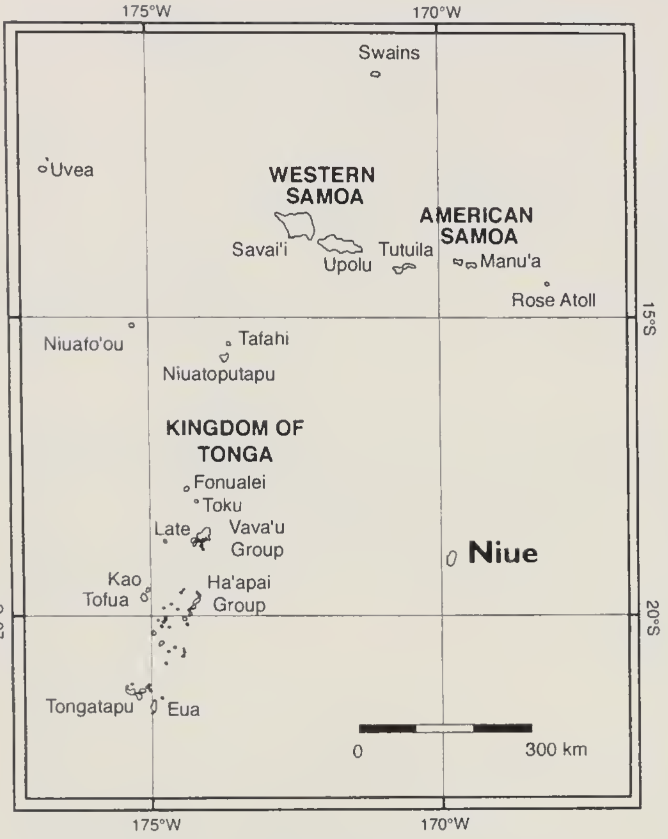


FIG. 1. The West Polynesian region.

METHODS

The Anakuli site.—As part of the Niue Archaeological Project (Walter and Anderson 1995), T.H.W. investigated 22 cave and rockshelter sites on Niue during 10 June–1 July 1994, January 1995, and 5 January–1 February 1996. The single site with appreciable prehistoric bird bones was Anakuli, a cave located behind Tuatea School at Hakupu Village (19° 07′ S, 169° 50′ W). The fauna from the other sites has been described elsewhere (Worthy et al. 1998). No vertebrate paleontological field research had taken place before on Niue, where a previous archaeological survey disclosed 59 unexcavated cave sites (Trotter 1979).

Anakuli has a round entrance about 2 m across that opens from a flat ground surface to a shaft about 4 m deep. The landing is the top of a talus cone in a chamber about 4 m across that slopes down on one side for about 6 m. The floor is covered by large coral boulders, derived from clearing the land above, as well as copious amounts of domestic rubbish. Because the site appeared to have potential as a pitfall trap for accumulating fossils of birds, an excavation was made at the lowest point of the chamber where the talus abutted the natural wall of the cave.

The overlying human refuse was cleared to reveal the original sediment surface of the cave. The upper layer (I) consisted of consolidated, water-rolled fragments of coral rubble 5–10 cm deep. Beneath this was Layer II, a loose deposit of fine reddish brown, soil-derived sediment containing coral rubble and bones in the upper 20 cm. Below this the sediment (Layer III) was clean coral rubble without soil or bones. Finally, flowstone deposits covered the floor of the cave. Bones of the Pacific rat (*Rattus exulans*) were found in Layer I but were absent from Layers II and III, suggesting a pre-Polynesian age for the bones of extinct birds, which were confined to Layer II. No prehistoric cultural materials were present in any of the layers.

An area of about 2.5 m^2 was excavated. The bone deposit was limited to an arc about 1 m long and 0.5 m wide along the cave's wall. Flowstone mounds on the floor confined the lateral extent of the deposit. Thus, the bones had accumulated in a hollow where water collected at the base of the talus slope.

Sixty-five bones representing five species of birds were recovered from Anakuli. Two of these species still live on Niue and will not be discussed further: *Porzana tabuensis*, represented by the distal end of a tarsometatarsus and the distal end of a tibiotarsus; and the distal end of a carpometacarpus of a columbid similar to that of *Ducula pacifica*. Most of the specimens from Anakuli belong to three species of birds that no longer occur on Niue and are the subject of this paper.

Radiocarbon dating.—A shaft of tibiotarsus and a shaft of tarsometatarsus of the new species of *Nycticorax* described below were submitted to the Rafter Radiocarbon Laboratory, Lower Hutt, New Zealand, for Accelerator-Mass Spectrometer (AMS) radiocarbon (^{14}C) dating. The interior and exterior of each bone were scraped, brushed, and rinsed with distilled water.

TABLE 1. Radiocarbon dating results (68% confidence intervals) from *Nycticorax* bones from Anakuli, Niue. Weight is the collagen yield after acid demineralization and the percent of collagen weight compared to the original bone weight. Radiocarbon age is uncalibrated and uncorrected for d^{13}C and given as years before present (yr BP). Calibrated age is corrected for d^{13}C, calibrated for atmospheric variation in ^{14}C, and presented in calendar years before present (CAL BP). NZA = Rafter Radiocarbon Laboratory, Lower Hutt, New Zealand.

Lab No.	Skeletal element	Weight (mg)	Radiocarbon age (yr BP)	d^{13} C	Calibrated age (CAL BP)
NZA5884	tibiotarsus	6 (1.4%)	4523 ± 92	−20‰	5277–4992
NZA5885	tarsometatarsus	34 (4%)	3447 ± 75	−20.3‰	3801–3795, 3723–3543, 3510–3495

The remaining bone was ground in a percussion mortar, sieved to 212 µm, and placed in acid (HCl) until effervescence ceased. The amount of collagen left in each sample (<50 mg) was insufficient to do a gelatin extraction, so the collagenous material was dated after this acid demineralization stage. This left the possibility of humic contamination in the dated samples, because humics are removed effectively only by gelatinization (Redvers-Newton and Coote 1994). Humic contamination may be minimal because the soils above the site are shallow, with little organic litter and no moss cover. Humates might contaminate the sample with older or, more likely, younger organic carbon, whereas possible carbonate contamination, although likely to be minor, would tend to make the apparent age older. Because neither of these samples meets the highest standards for AMS ^{14}C dating of bone (see Stafford et al. 1988, 1991), we regard the radiometric chronology of the bone deposit at Anakuli to be tentative.

The two bones of *Nycticorax* new sp. from Anakuli yielded mid-Holocene ^{14}C dates in the neighborhood of 5300 and 3600 years old (Table 1). These age determinations are reasonable given that the dated bones were recovered below the bones of *Rattus exulans,* an introduced species that first arrived in nearby Tonga about 2800 years ago (D.W.S. and D. V. Burley, pers. obs.) and is unlikely to have lived on Niue any earlier.

Techniques.—The prehistoric bones are catalogued in the collections of the National Museum of New Zealand Te Papa Tongarewa (MNZ). Skeletons used in our comparisons are from MNZ, Florida Museum of Natural History (UF), U.S. National Museum of Natural History (USNM), University of Michigan Museum of Zoology (UMMZ), and University of Washington Burke Museum (UWBM). The following skeletons were used for intergeneric comparisons of ardeids: *Ardea sumatrana* USNM 488342; *A. alba* USNM 610600; *A. pacifica* USNM 613003; *A. novaehollandiae* MNZ 12684, USNM 613003; *Egretta sacra* UF 39393, USNM 560712, UWBM 42724, 42783; *Butorides striatus* USNM 559813; *Botaurus poeciloptilus* USNM 502126; *B. stellaris* USNM 502140; *Ixobrychus sinensis* UF 38131, 39923; *I. flavicollis* UF 39524; *Nycticorax caledonicus* USNM 558301; *Nycticorax nycticorax* MNZ 19310, UF 35841; and *N. (Nyctanassa) violacea* UF 22905. Specimens measured in Tables 3–5 are as follows: *Nycticorax* new species MNZ 537651, 37692; *N.* undescribed species (‘Eua) UF 52971; *N. caledonicus* USNM 556979, 558301, 561542, 612629, UMMZ 224713; *N. nycticorax hoactli* USNM 289884, 431388, 431964, 432698, 488680, 489903, 499390, 501635, 501991, 610608, 610609, UF 22900, 22901, 35841; *N. n. nycticorax* USNM 292037, 319467, 430526, 430527, UF 11440, 11453, 2897, 22899; *N. violacea* USNM 18028, 18501, 318841, 491403, 502477, 558045, 611552, UF 11447; *N. leuconotus* UMMZ 201761; *Megapodius pritchardii* MNZ 37701, 37702, 37706, 37707, USNM 319633, 319634; *M. freycinet* USNM 556998, 557007, 557015, 557018; *M. eremita* UF 40180; *M. alimentum* UF 51879, 57791, 57792, 57795, 57796, 57916, BPBM 165670; *Gallirallus* new species MNZ S37708, 37709, 37710, 37711; *G. ripleyi* UF 51320, 51499, 53933, 53936, 53939, 53997, 54287, 54352, 54529, USNM 402895; *G.* undescribed sp. ‘Eua UF 51729, 51734, 51735, 51991, 52058, 52137, 52354, 52518; *G. philippensis* MNZ 25267, UWBM 42863, 42865, 42866, UF 39854, 39855.

Prehistoric bones of *Nycticorax, Megapodius,* and *Gallirallus* from Tonga and the Cook Islands are primarily from UF, with smaller collections from USNM. Osteological nomenclature usually follows Baumel and coworkers (1993). Measurements were taken with digital calipers with 0.01 mm increments, rounded to the nearest 0.1 mm.

SYSTEMATIC PALEONTOLOGY

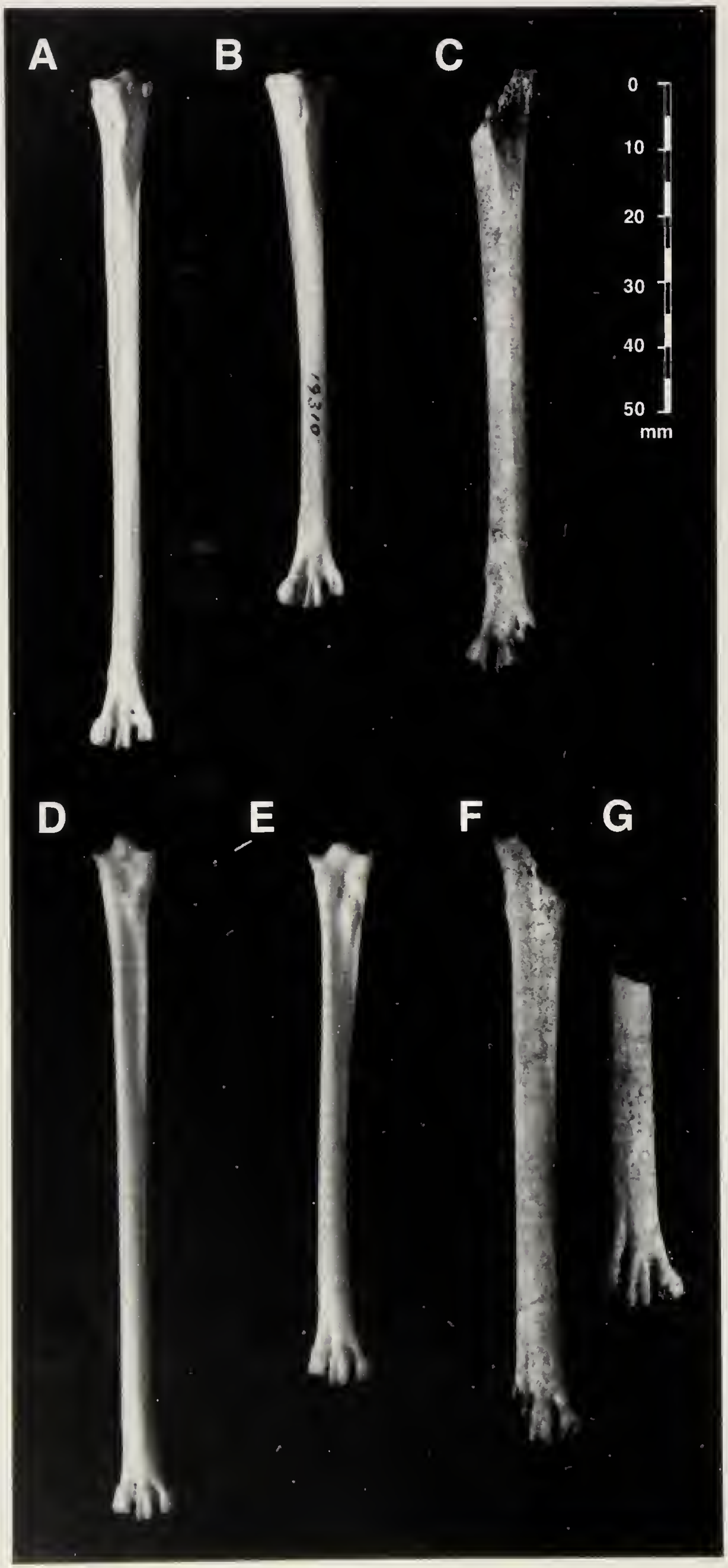
Order Incertae sedis (Olson 1985)

Family Ardeidae

Genus *Nycticorax* Rafinesque

The holotypical tarsometatarsus of the new species is referred to *Nycticorax* (including *Nyctanassa* but excluding *Calherodius* and *Gorsachius*; for various opinions on generic classification of night-herons see Payne and Risley 1976, Sheldon et al. 1995) rather than other genera of Ardeidae because of the following combination of characters: trochlea metatarsi IV slightly grooved distally; more proximal placement of distal foramen relative to proximal end of trochlea metatarsi III; parallel orientation of trochlea metatarsi III with shaft; gradual protruding of trochlea metatarsi II from corpus tarsometatarsi; distal foramen small; medial side compressed, especially proximally, to a narrow flange; anteriorly, distal to the tuberositas musculo tibialis cranialis, the bone is flat and slopes medially (not markedly concave as in *Ardea*); posteriorly, the shaft is convex with a weak intermuscular line laterally placed (in *Ardea* the shaft is concave and the intermuscular line is prominant and laterally placed and in *Botaurus* the shaft is concave with a prominant intermuscular line centrally placed).

All other elements of the new species also have characters of *Nycticorax* rather than of other ardeid genera. Notable among these characters are: mandible with medial groove bridged by an oblique ridge; coracoid with relatively slender shaft, dorsal surface of sternal end deeply concave, and the ridge between the facies articularis humeralis and processus acrocoracoideus very steep in dorsal view; scap-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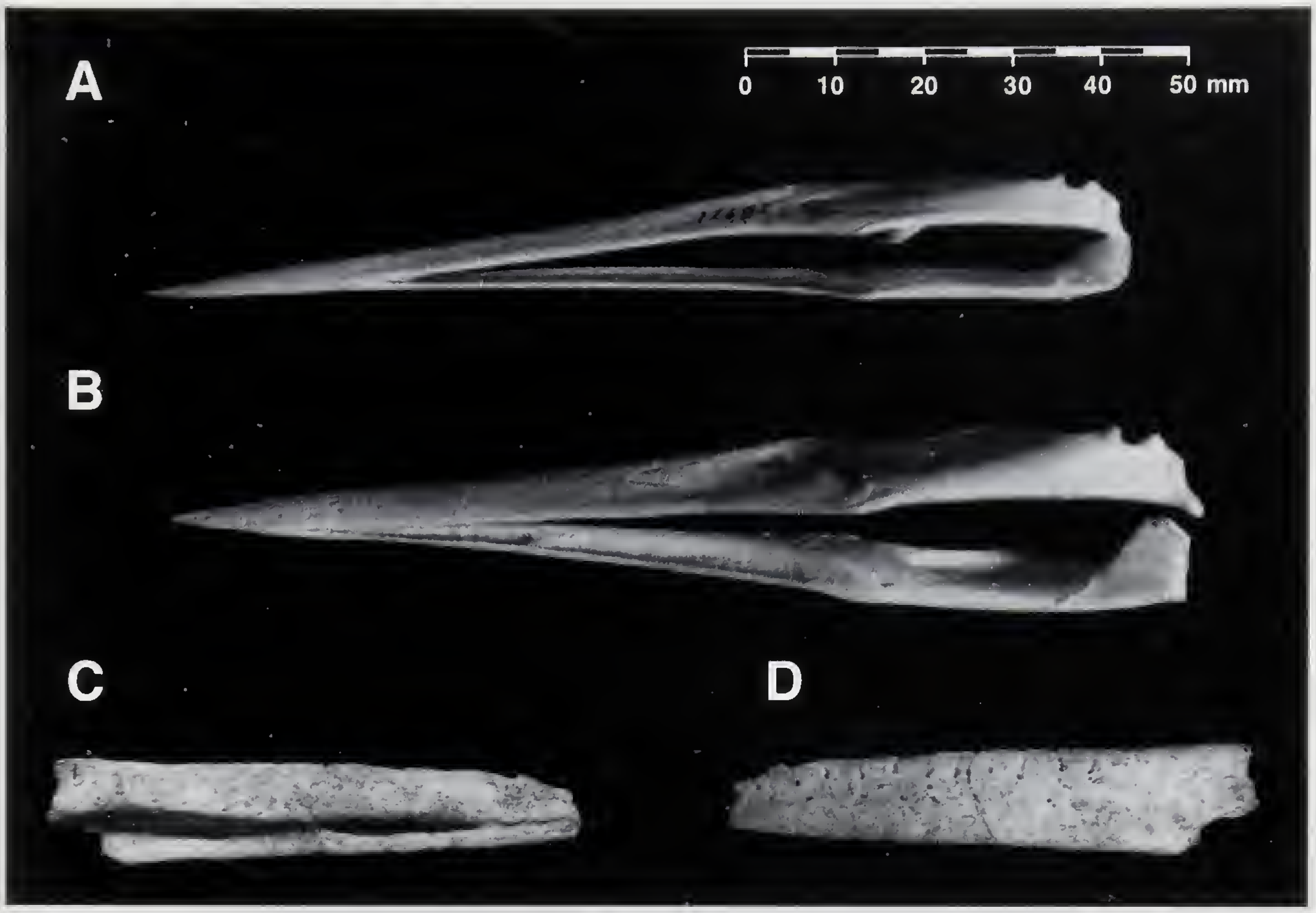

FIG. 3. The mandible of herons in lateral (A, B, D) and medial (C) aspects. A. *Ardea novaehollandiae* MNZ 12684. B. *Nycticorax caledonicus* MNZ 19310. C, D. *Nycticorax kalavikai*, new species, MNZ S37653.

ula with the facies articularis clavicularis rising dorsally from the plane of the shaft (dorsal margin straight in *Ardea* and *Egretta*) and rounded proximo-dorsally (pointed in *Ardea* and *Egretta*); carpometacarpus with processus extensorius directed more medially (more proximally in *Ardea* and *Egretta*), and the os metacarpi alulare with a marked fossa; tibiotarsus with smooth posterior edge to area interarticularis (notched in *Ardea, Egretta,* and *Botaurus*).

***Nycticorax kalavikai*,** new species

Holotype.—MNZ S37651, tarsometatarsus (Fig. 2, Table 3), collected by T. H. Worthy on 7–12 January 1995 at Anakuli, Niue.

Topotypical paratypes.—MNZ S37652–S37700, occipital fragment of cranium, pterygoid, 4 incomplete mandibles (Fig. 3), coracoid (Fig. 4), 2 scapulae (Fig. 5), anterior portion of sternum, 4 cervical vertebrae (numbers 6, 10, 11, 12), thoracic vertebra (number 17), distal humerus, 2 distal and 1 complete ulnae (Fig. 6), 1 distal and 2 proximal radii, 4 proximal and 3 shafts of carpometacarpi (Fig. 7), pelvis, 3 femoral shafts, 3 distal and 1 proximal tibiotarsi (Fig. 8), 8 tarsometatarsi, pedal digit I (phalanx 1), pedal digit III (phalanx 2), pedal digit IV (phalanx 1). Minimum of four individuals. Selected measurements of paratypes are as follows: coracoid: length 52.7 mm; radius: distal width 7.8 mm; ulna: total length: 123 mm, proximal width 10.6 mm, width of shaft 5.3 mm, depth of shaft 4.9 mm, distal width 7.6, 7.8, 8.4 mm; carpometacar-

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FIG. 2. The tarsometatarsus of herons in plantar (A–C) and a acrotarsial (D–G) aspects. A, D. *Ardea novaehollandiae* MNZ 12684. B, E. *Nycticorax caledonicus* MNZ 19310. C, F. *Nycticorax kalavikai*, new species, MNZ S37651, holotype. G. *Nycticorax kalavikai*, new species, MNZ S37652.


A
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C
D
E
F
G
H
I
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20
30
40
50

FIG. 5. The scapula of herons in dorso-medial aspect. A. *Ardea novaehollandiae* MNZ 12684. B. *Nycticorax caledonicus* MNZ 19310. C. *Nycticorax kalavikai,* new species, MNZ S37658.

pus: proximal width 12.4 mm; femur: width of shaft 6.3, 6.3, 6.4 mm, depth of shaft 6.4, 6.6, 6.6 mm; tibiotarsus: proximal width 11.8 mm, proximal depth 13.8 mm, minimum width of shaft 6.1, 5.8, 6.1, 5.3 mm, distal width 12.4, 11.4 mm.

Diagnosis.—A large species of *Nycticorax* that differs from living congeneric species in these major features (see Table 2 for comparative details and additional characters in all extant species of *Nycticorax*): rostrum narrower and straighter; dentary thicker and deeper overall with deep median groove; sternum with double foramen pneumaticum; coracoid with more rounded ventro-humeral and laterohumeral portions of shaft, more deeply excavated in the triosseal canal dorso-mediad of the facies articularis humeralis than in *N. caledonicus,* and facies articularis clavicularis larger, overlapping the shaft more; scapula with more rounded facies articularis humeralis; ulna shorter (relative to leg elements) than in *N. caledonicus,* with less prominent papillae remigiales caudales, more dorso-ventrally expanded shaft, larger tuberculum carpale that encloses a marked fossa between it and the condylus ventralis ulnaris, and a longer condylus dorsalis ulnaris; carpometacarpus with deeper fossa supratrochlearis, shorter overall; femur, tibiotarsus, and tarsometatarsus stouter; tarsometatarsus with fossa infracotylaris dorsalis relatively shallower.

Etymology.—From the Niuean words *kalavi* (land crab) and *kai* (food; see McEwen 1970). The name *kalavikai* alludes to our speculation that land crabs, typically abundant on raised limestone islands in Oceania, may have been an important food for this extinct night-heron.

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FIG. 4. The coracoid of herons in dorsal (A–C), ventral (D–F), and lateral (G–I) aspects. A, D, G. *Ardea novaehollandiae* MNZ 12684. B, E, H. *Nycticorax caledonicus* MNZ 19310. C, F, I. *Nycticorax kalavikai,* new species, MNZ S37657.

TABLE 2. Osteological character summary for species of *Nycticorax*.

Skeletal element Character	*N. kalavikai*	*N. caledonicus*	*N. nycticorax*	*N. violacea*	*N. leuconotus*
PTERYGOID					
Stoutness	medium	stout	stout	slender	slender
Dorsal surface	barely concave	very concave	very concave	very concave	barely concave
ROSTRUM					
Shape in dorsal aspect	narrow	narrow	broad	narrow	narrow
Shape in lateral aspect	straight, tapers less gradually	curved, tapers gradually	curved, tapers gradually	curved, tapers gradually	curved, tapers gradually
DENTARY					
Overall depth	deep	shallow	shallow	shallow	shallow
Medial groove	deep	deep	shallow	deep	deep
Angle of cutting surface	acute	more obtuse	acute	more obtuse	more obtuse
Lateral surface	±flat	±flat	flat-convex	concave	±flat
STERNUM					
Dorso-ventral compression of sulcus articularis coracoideus	more	less	less	less	less
Foramen pneumaticum	double	double	single	single	single
CORACOID					
Ventro-humeral & latero-humeral portion of shaft	rounded	rounded	sharper	sharper	rounded
Sulcus musculo supracoracoideus	deep	deep	shallow	deep	deep
SCAPULA					
Facies articularis humeralis	rounded	intermediate	oblong	oblong	oblong

TABLE 2. CONTINUED.

Skeletal element Character	*N. kalavikai*	*N. caledonicus*	*N. nycticorax*	*N. violacea*	*N. leuconotus*
ULNA					
Papillae remigiales caudales	weak	weak	strong	strong	weak
Dorso-ventral expansion of shaft	more	more	less	less	less
Tuberculum carpale	large	small	small	small	small
Condylus dorsalis ulnaris	long	short	short	short	long
CARPOMETACARPUS					
Fossa supratrochlearis	deep	intermediate	shallow	shallow	shallow
Processus pisiformis in proximal aspect	large	small	small	small	small
Length relative to ulna	short	long	long	long	long
FEMUR					
Overall shape	stout	intermediate	slender	slender	slender
TIBIOTARSUS					
Overall	stout	stout	slender	slender	slender
Incisura intercondylaris between distal margin of condyles	more concave	less concave	less concave	less concave	less concave
TARSOMETATARSUS					
Overall shape	stout	stout	slender	stout	slender
Dorso-ventral compression of proximo-medial margin of shaft	intermediate	compressed	thickened	compressed	compressed

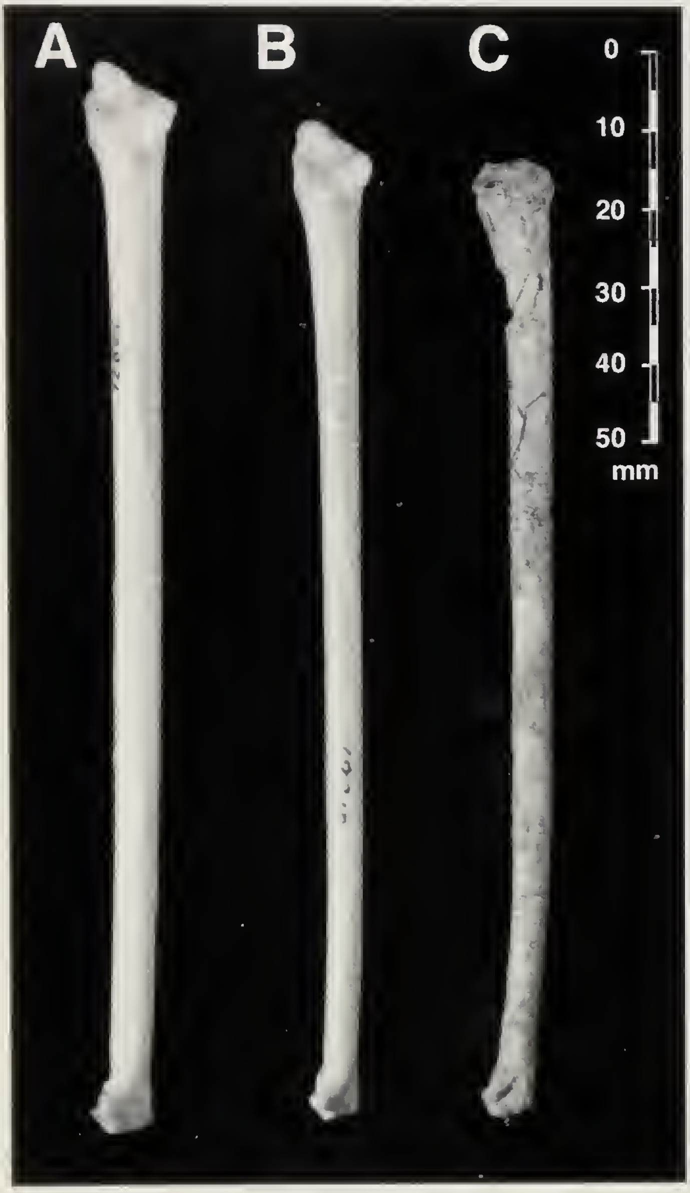

FIG. 6. The ulna of herons in medial aspect. A. *Ardea novaehollandiae* MNZ 12684. B. *Nycticorax caledonicus* MNZ 19310. C. *Nycticorax kalavikai*, new species, MNZ S37667.

Crustaceans are a regular part of the diet in living species of *Nycticorax* (Martínez-Vilalta and Motis 1992).

Remarks.—Although males average slightly larger than females in most linear skeletal measurements in *Nycticorax nycticorax* and *N. violacea*, the overlap is considerable (Adams 1955) and we do not consider sexual dimorphism to be an important factor in evaluating the measurements of fossil night-herons. We agree with Payne and Risley (1976) that *N. nycticorax* and *N. caledonicus* are similar osteologically, and are more similar to *N. kalavikai* in having a narrower bill than in *N. violacea*. Because it shares more characters with *N. kalavikai* than with other species, *N. caledonicus* is probably the closest living relative of *N. kalavikai*, as might be suspected on geographical grounds.

Nycticorax kalavikai is known thus far only from Niue. It is the first extinct species of *Nycticorax* to be described from Polynesia. From a cave on the Tongan island of ‘Eua, however, D.W.S. has recovered three bones (rostrum, tarsometatarsus, pedal phalanx) of another extinct, late Quaternary species of *Nycticorax*. The undescribed species from ‘Eua is included in faunal lists by Steadman (1993a, 1995) and measurements given in Table 3; it will be described by D.W.S. in a separate paper. In the Mascarene Islands (Indian Ocean), three endemic, allopatric species of *Nycticorax* became extinct since human arrival about 500 years ago (Mourer-Chauviré et al. 1999). Unlike the Polynesian forms, two of the three Mascarene species had relatively small wings and may have been flightless. An undescribed, extinct form of *Nycticorax* is known as well from Ascension Island in the Atlantic Ocean (S. L. Olson 1977, pers. comm.).

Order Galliformes

Family Megapodiidae

Genus *Megapodius* Quoy and Gaimard

Megapodius pritchardii Gray

Material.—MNZ S37701–S37707, proximal carpometacarpus, 2 femora (Fig. 9), 1 proximal and 2 distal tarsometatarsi (Fig. 10), pedal phalanx, collected at Anakuli, Niue by T. H. Worthy on 7–12 January 1995. Minimum of two individuals.

Remarks.—This material resembles modern skeletons of *Megapodius pritchardii* (from Niuafo’ou, Tonga) in all qualitative features. The Niuean bones average slightly larger than in two modern specimens of *M. pritchardii* (Table 4) but are distinctly smaller than in the living *M. freycinet* sensu lato (Moluccas through Vanuatu) and the extinct *M. alimentum* of Tonga (Steadman 1989). The fossil femur from Niue resembles that of *M. pritchardii* and differs from that of *M. freycinet* in that the distal medial condyle is markedly longer than deep in medial aspect, rather than being about as deep as long.

The only other record of a megapode from as far east as Niue is from an archaeological site on Ofu, American Samoa (Steadman

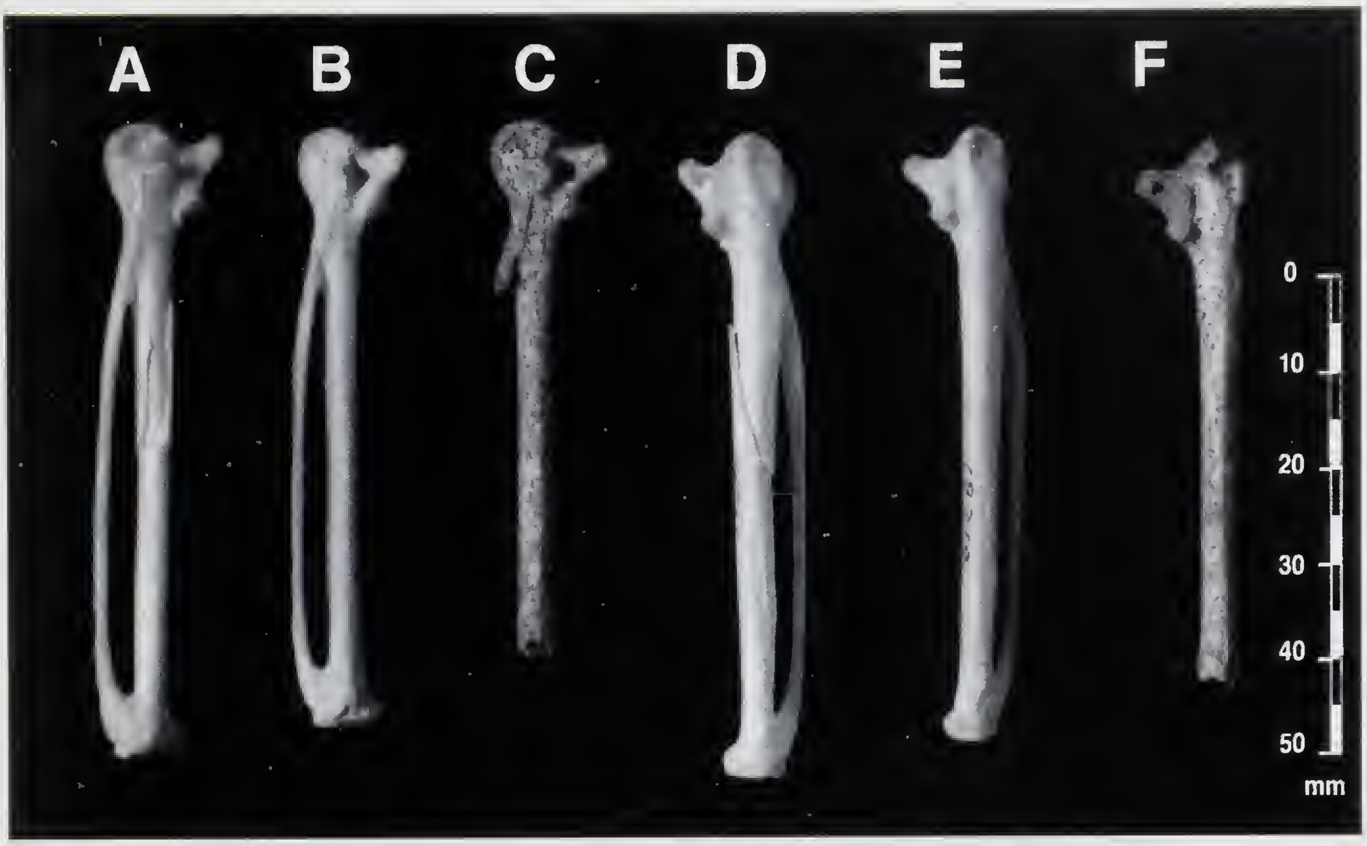

FIG. 7. The carpometacarpus of herons in ventral (A–C) and dorsal (D–F) aspects. A, D. *Ardea novaehollandiae* MNZ 12684. B, E. *Nycticorax caledonicus* MNZ 19310. C, F. *Nycticorax kalavikai*, new species. MNZ S37673.

1993b). The limited material from Ofu (fragmentary ulna and femur) is in the small size range of *M. freycinet* sensu lato, and is larger than in *M. pritchardii*. Until more material is available, however, we cannot be certain whether these two easternmost records of megapodes represent the same or different species.

Order Ralliformes (Gruiformes)
Family Rallidae
Genus *Gallirallus* Lafresnaye

Gallirallus huiatua, new species

Holotype.—MNZ S37708, tarsometatarsus (Fig. 11), collected at Anakuli, Niue by T. H. Worthy on 7–12 January 1995.

Topotypical paratypes.—MNZ S37709–S37711, proximal ulna, shaft of femur, distal tibiotarsus (Fig. 12). Minimum of one individual.

Diagnosis.—A medium-sized (Table 5) species of *Gallirallus* that differs from congeners as follows. Ulna more dorso-ventrally compressed than in *G. philippensis*. In cranial aspect, femur with mid-shaft relatively straight as in *G. philippensis* (constricted in *G. ripleyi* and *G.* undescribed sp. from ‘Eua) and distal half of shaft of intermediate stoutness as in *G. ripleyi* (thickened in *G.* undescribed sp. from ‘Eua, narrow in *G. philippensis*). Tibiotarsus with deep incisura intercondylaris as in *G.* undescribed sp. from ‘Eua (shallow in *G. ripleyi,* intermediate to deep in *G. philippensis*) and flat disto-dorsal portion of shaft as in *G. ripleyi* (concave in *G.* undescribed sp. from ‘Eua and *G. philippensis*). Tarsometatarsus slender overall as in *G. philippensis* (stout in *G. ripleyi* and *G.* undescribed sp. from ‘Eua), with shallow shaft (deep in the others), and flat disto-dorsal surface of shaft (concave in *G.* undescribed sp. from ‘Eua and *G. philippensis,* intermediate to concave in *G. ripleyi*).

Etymology.—From the Niuean compound word *hui-atua,* which means “the bones [*hui*] of the dead [*atua*]” (Smith 1902:207).

Remarks.—The morphology of *Gallirallus huiatua* does not argue for a closer relationship to any one species than another, including the two geographically nearest congener-

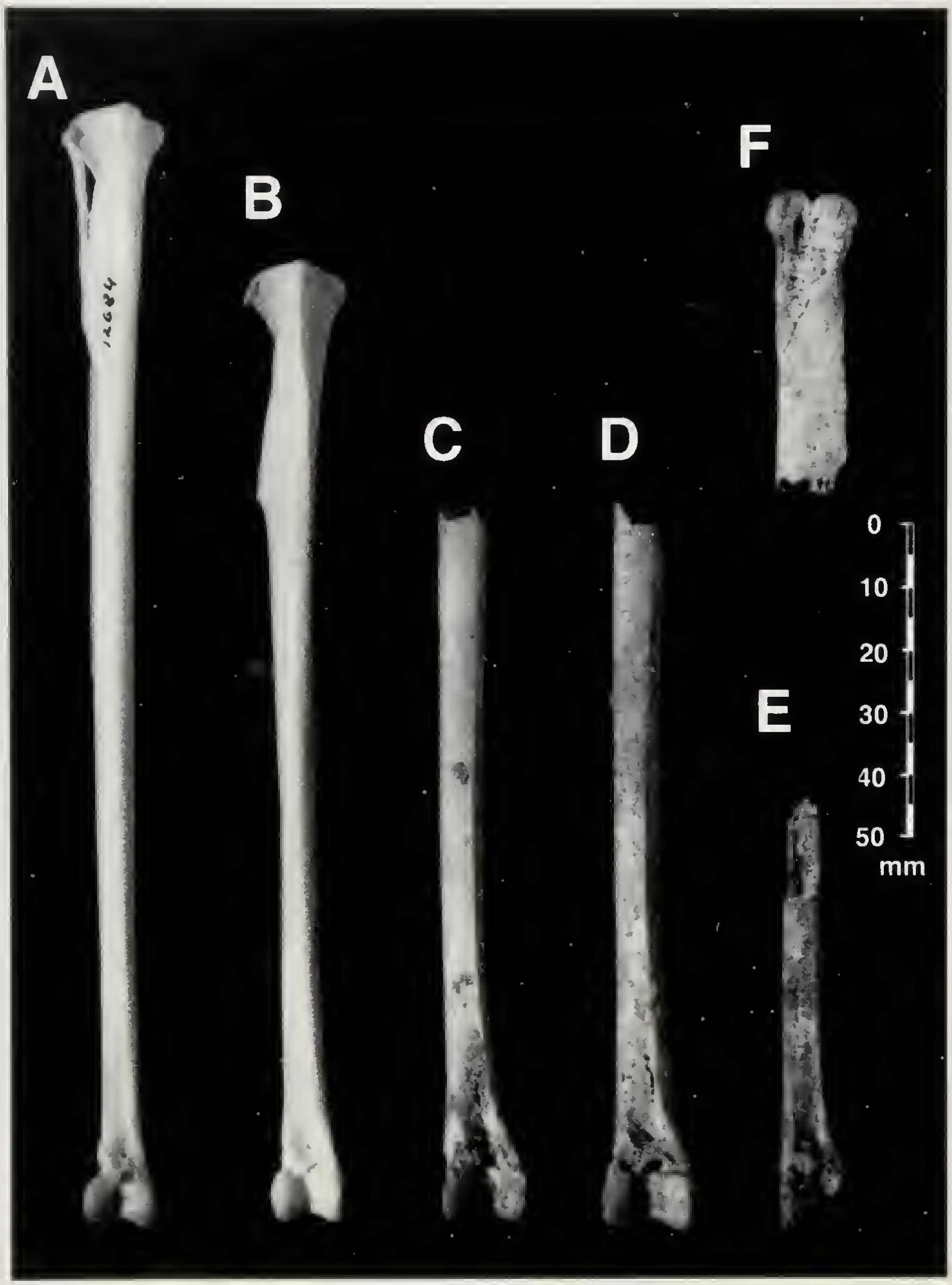

FIG. 8. The tibiotarsus of herons in dorsal aspect. A. *Ardea novaehollandiae* MNZ 12684. B. *Nycticorax caledonicus* MNZ 19310. C–F. *Nycticorax kalavikai*, new species, MNZ S37683–S37686.

ic flightless species, *G. ripleyi* of Mangaia (Steadman 1987) and *G.* undescribed species of ‘Eua (Steadman 1993a). Selected intra-elemental ratios (C/A of ulna; B/A, C/A, D/A of femur) and inter-elemental ratios [C(ulna)/C(femur)] in Table 5 suggest that *G. huiatua* was flightless. The widespread, volant *G. philippensis* occurs on Niue today. Unlike its flightless congeners, *G. philippensis* is unknown on remote islands of Oceania before the arrival of people (Steadman 1993a, 1995).

DISCUSSION

The West Polynesian (Fiji, Tonga, Samoa) rather than East Polynesian affinities of the Niuean avifauna are strengthened by the addition of *Nycticorax kalavikai* and *Megapodius pritchardii*. Neither genus is known on islands east of Niue. The nearest localities with resident species of *Nycticorax* are New Caledonia (*N. c. caledonicus*), the Solomon Islands (*N. c. mandibularis*), Palau (*N. c. pelewensis*; Peters 1930, Martínez-Vilalta and Motis 1992), and prehistorically in Tonga

TABLE 3. Measurements (in mm) of the tarsometatarsus in *Nycticorax*, with mean, range, and sample size. SU, sex unknown. The measurements of *N. caledonicus* include the subspecies *N. c. hilli* and *N. c. caledonicus*.

	N. kalavikai, new sp. (SU) Niue	*N.* undescribed sp. (SU) 'Eua, Tonga	*N. caledonicus* (2M, 3F) Halmahera, Australia, New Caledonia	*N. nycticorax hoactli* (8M, 6F) North America, Bolivia	*N. n. nycticorax* (4M, 3F, SU) France, Zaire, Zimbabwe, China, Japan	*N. violacea* (M, F, SU) Florida, Haiti, Barbuda, Swan Is., Panamá, Galápagos	*N. leuconotus* (F) Zambia
TARSOMETATARSUS							
Distal width	12.6	13.1	10.8	11.1	9.5	10.3	8.3
			10.0–11.7	10.5–12.0	9.1–10.3	9.5–10.9	
	1	1	5	14	8	8	1
Width of middle trochlea	3.9	3.9	3.3	3.4	2.9	3.1	2.5
	3.9		3.0–3.6	3.1–3.7	2.7–3.1	2.7–3.4	
	2	1	5	14	8	8	1
Depth of middle trochlea	—	7.6	6.2	6.3	5.6	5.6	4.9
			6.0–6.3	6.0–6.7	5.4–6.1	5.3–6.1	
		1	5	14	8	8	1
Width of shaft at distal foramen	9.0	9.3	6.9	7.4	6.2	7.2	5.8
	8.8–9.0		6.5–7.2	6.8–8.0	5.9–6.6	6.8–7.7	
	2	1	5	14	8	8	1
Depth of shaft at distal foramen	4.0	4.5	3.2	3.2	2.9	2.8	2.5
	3.9–4.1		3.1–3.6	2.9–3.5	2.8–3.1	2.7–3.0	
	2	1	5	14	8	8	1

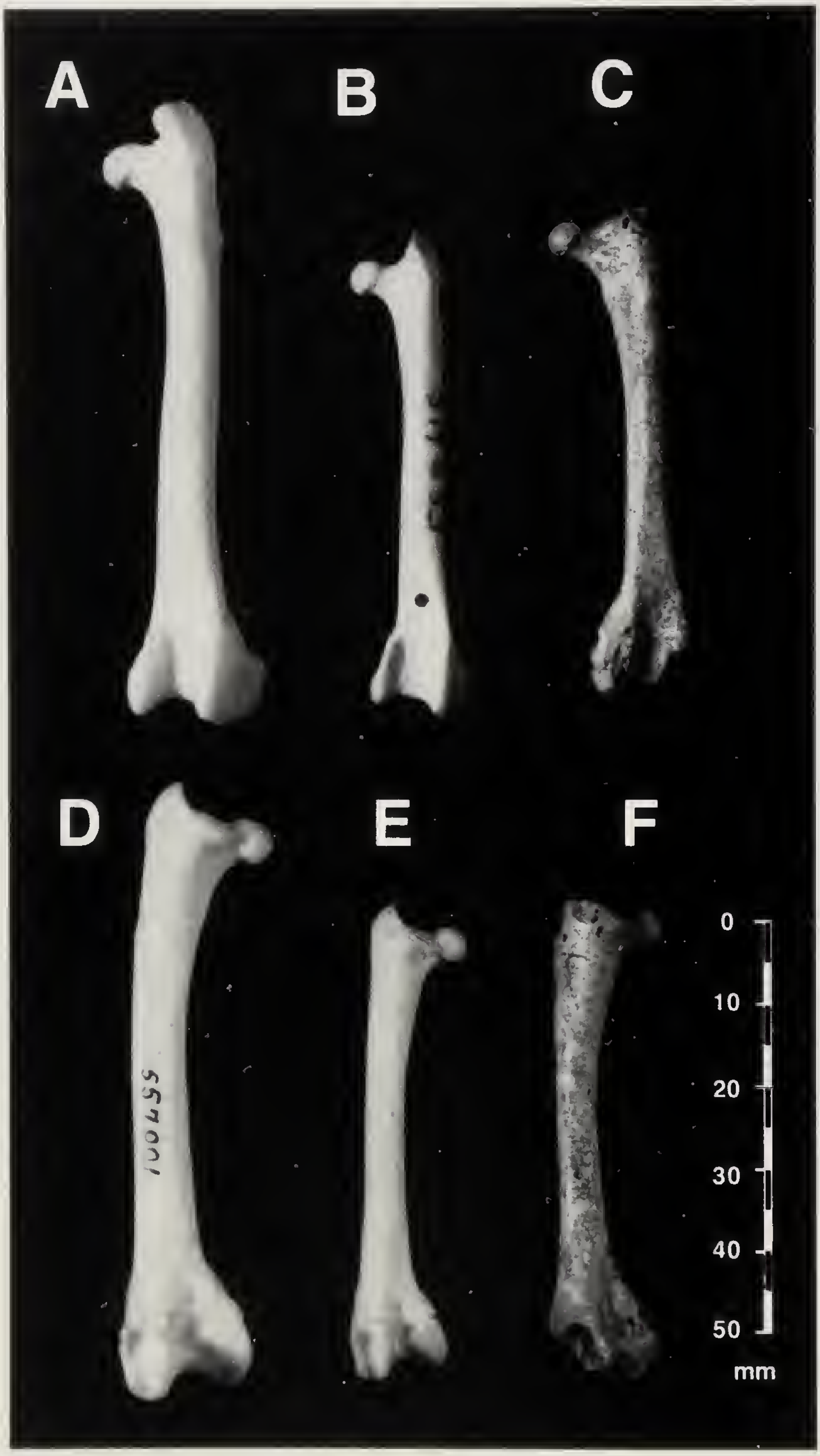

FIG. 9. The femur of *Megapodius* in dorsal (A–C) and ventral (D–F) aspects. A, D. *M. freycinet*, USNM 557001. B, E. *M. pritchardi*, USNM 319633. C, F. *M. pritchardii*, MNZ S37702.

(Steadman 1993a). The nearest localities for *Megapodius* are Tonga (*M. pritchardii* and three extinct species) and American Samoa (*Megapodius* sp., near *M. freycinet* s.l.; Steadman 1999). *Gallirallus huiatua* is not similar to any of the flightless species of *Gallirallus* known thus far. Morphological and phylogenetic details of the radiation of flightless species of *Gallirallus* across the tropical Pacific remain poorly understood.

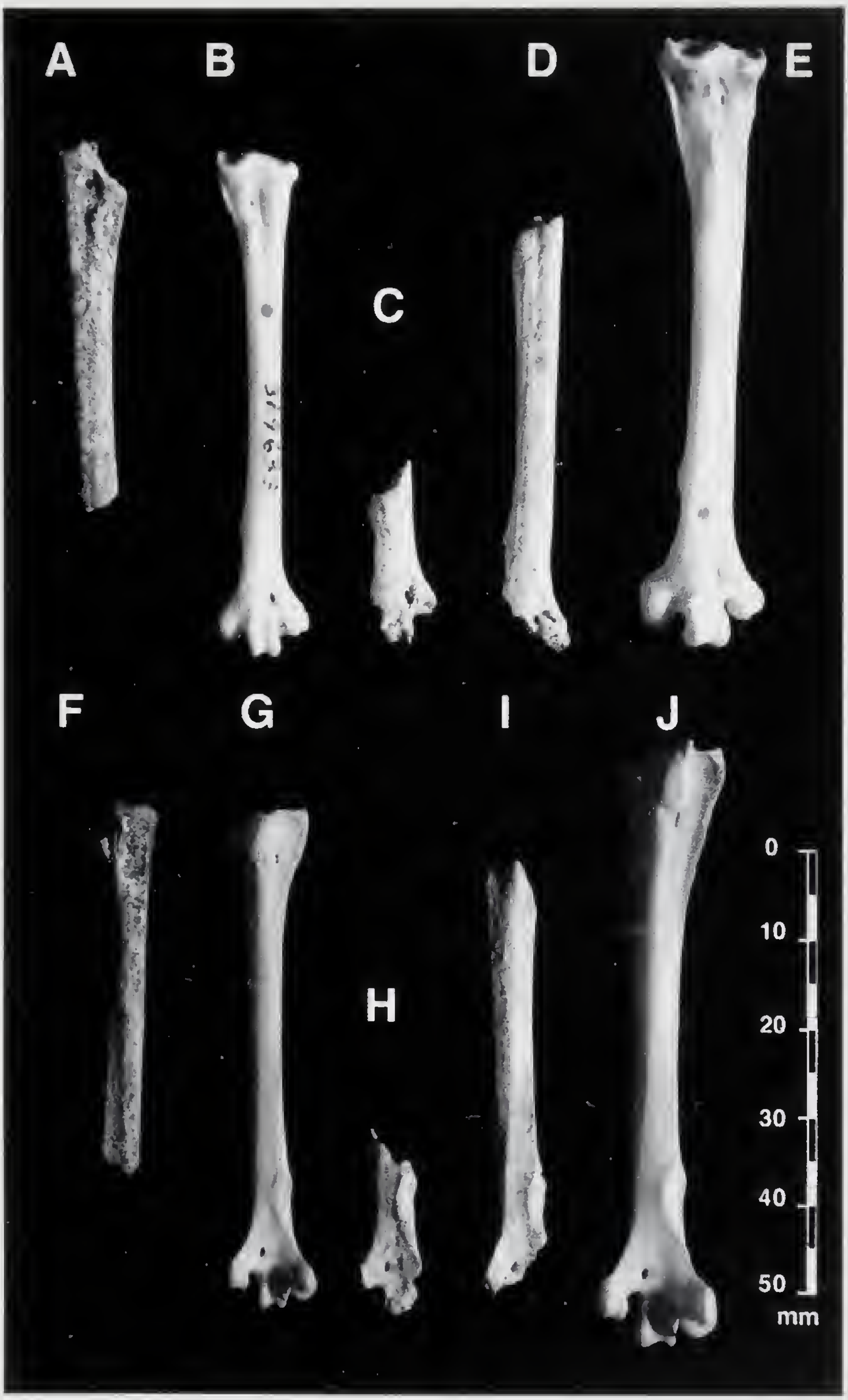

FIG. 10. The tarsometatarsus of *Megapodius* in acrotarsial (A–E) and plantar (F–J) aspects. A, C, D, F, H, I. *M. pritchardii*, MNZ S37704–S37706. B, G. *M. pritchardii*, USNM 319633. E, J. *M. freycinet* USNM 557001.

Hunting (see Loeb 1926) and habitat loss may have been involved in the loss of night-herons, megapodes, and flightless rails on Niue (as is believed to be the case on other oceanic islands; Steadman 1995), although the bones from Anakuli provide no direct evidence of this. The absence of rat bones in Layer II of Anakuli suggests that the bones analyzed herein were deposited before people arrived on Niue, which is supported by the two radiocarbon dates obtained on bones of *Nycticorax kalavikai*. The likely calendar age

TABLE 4. Measurements (in mm) of the carpometacarpus, femur, tarsometatarsus, and pedal digit III, phalanx 1 of *Megapodius*, with mean, range, and sample size.

	M. pritchardii Niue (SU)	*M. pritchardii* Niuafo'ou, Tonga (SU)	*M. freycinet* Halmahera, Indonesia (2M, 2F)	*M. eremita* Isabel, Simbo, Solomon Islands (3F, SU)	*M. alimentum* Ha'apai, Tonga (SU)	*M. alimentum* 'Eua (SU)
CARPOMETACARPUS						
Least width of shaft	2.7	2.5	3.1	3.0	—	—
		2.4–2.6	2.9–3.2	2.7–3.2		
	1	2	4	4		
Least depth of shaft	3.3	3.0	4.0	3.9	—	—
		3.0	3.8–4.2	3.7–4.3		
	1	2	4	4		
FEMUR						
Total length	53.1	49.4	64.9	66.8	70.2+	—
		49.0–49.9	62.5–67.7	64.1–68.7	70.0+	
	1	2	4	4	70.5+	
					3	
Least width of shaft	4.5	4.4	6.4	5.9	6.5	—
		4.2–4.5	6.0–6.7	5.7–6.1	6.2–7.0	
	1	2	4	4	3	
Least depth of shaft	4.7	4.5	6.1	5.3	6.3	—
		4.3–4.7	5.6–6.6	4.6–5.5	5.9–6.5	
	1	2	4	4	3	
TARSOMETATARSUS						
Least width of shaft	4.5	3.9	5.6	5.3	5.8	—
	4.3–4.7	3.9	5.1–6.2	5.1–5.4	5.5–6.2	
	2	2	4	3	3	
Least depth of shaft	2.7	2.5	3.4	3.4	3.5	—
	2.7	2.4–2.6	3.1–3.6	3.3–3.4	3.3–3.7	
	2	2	4	3	3	

TABLE 4. CONTINUED.

	M. pritchardii Niue (SU)	*M. pritchardii* Niuafo'ou, Tonga (SU)	*M. freycinet* Halmahera, Indonesia (2M, 2F)	*M. eremita* Isabel, Simbo, Solomon Islands (3F, SU)	*M. alimentum* Ha'apai, Tonga (SU)	*M. alimentum* 'Eua (SU)
PEDAL DIGIT III, PHALANX 1						
Total length	14.3	13.8	17.4	15.6	—	20.0
		13.7–13.8	17.1–17.7	14.6–16.9		
	1	2	4	3		1
Proximal width	4.6	4.2	5.7	5.5	—	7.8
		4.2	5.4–6.0	5.4–5.6		
	1	1	4	3		1
Proximal depth	4.3	3.6	5.4	4.9	—	6.7
		3.6–3.7	5.2–5.7	4.6–5.2		
	1	2	4	3		1
Least width of shaft	2.8	2.4	3.4	3.2	—	4.4
		2.4–2.5	3.2–3.6	3.2–3.3		
	1	2	4	3		1
Least depth of shaft	2.1	1.8	2.8	2.6	—	3.4
		1.8–1.9	2.4–3.0	2.5–2.6		
	1	2	4	3		1
Distal width	3.3	2.9	4.1	3.7	—	5.3
		2.8–3.0	3.7–4.3	3.7–3.8		
	1	2	4	3		1
Distal depth	3.5	2.8	4.2	3.8	—	5.2
		2.8	4.0–4.3	3.7–3.9		
	1	2	4	3		1

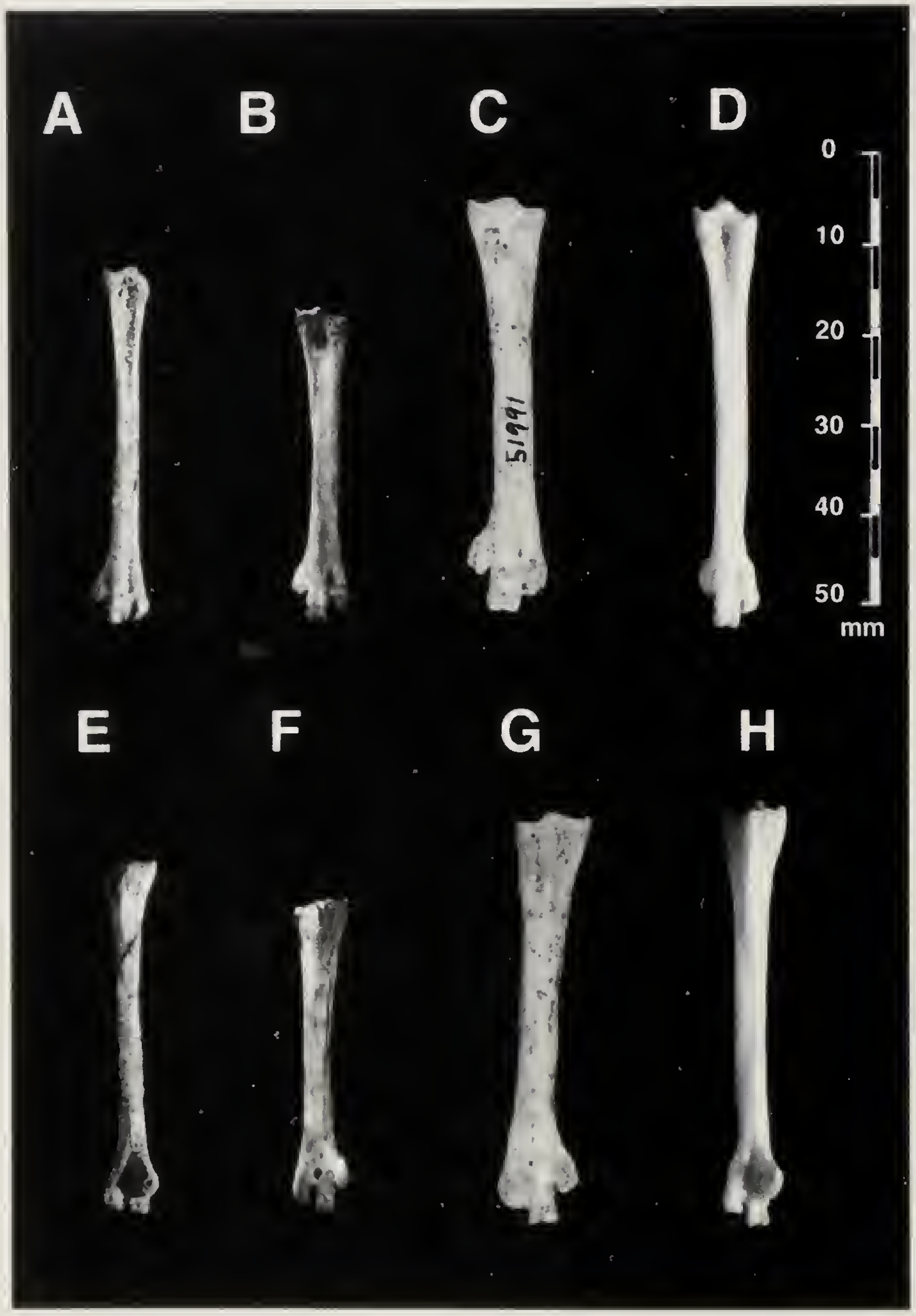

FIG. 11. The tarsometatarsus in acrotarsial (A–D) and plantar (E–H) aspects of *Gallirallus*. A, E. *G. huiatua*, MNZ S37708, holotype. B, F. *G. ripleyi*, USNM 402895. C, G. *G.* new sp., UF 51991 ('Eua, Tonga). D, H. *G. philippensis*, MNZ 25267.

range of about 5300 to 3600 years ago is about 1500 years older than the oldest archaeological remains on Niue (Walter and Anderson 1995).

Our sampling of the pre-human avifauna of Niue is very incomplete. The pitfall nature of Anakuli probably explains why the site collected mainly ground-dwelling species such as herons, megapodes, and rails. Arboreal species, such as pigeons, doves, parrots, and passerines, must also have been part of the pre-human avifauna of Niue but are poorly represented in the bone deposit. As many as 20 other extirpated species of birds, still unrecorded, are likely to have been present on Niue before human arrival, if the much more extensive pre-cultural fossil records from adjacent island groups (Tonga, Cook Islands) are any indication (Steadman 1993a, 1995). A more complete picture of the avifauna that greeted the first people on Niue awaits the discovery of other bone deposits.

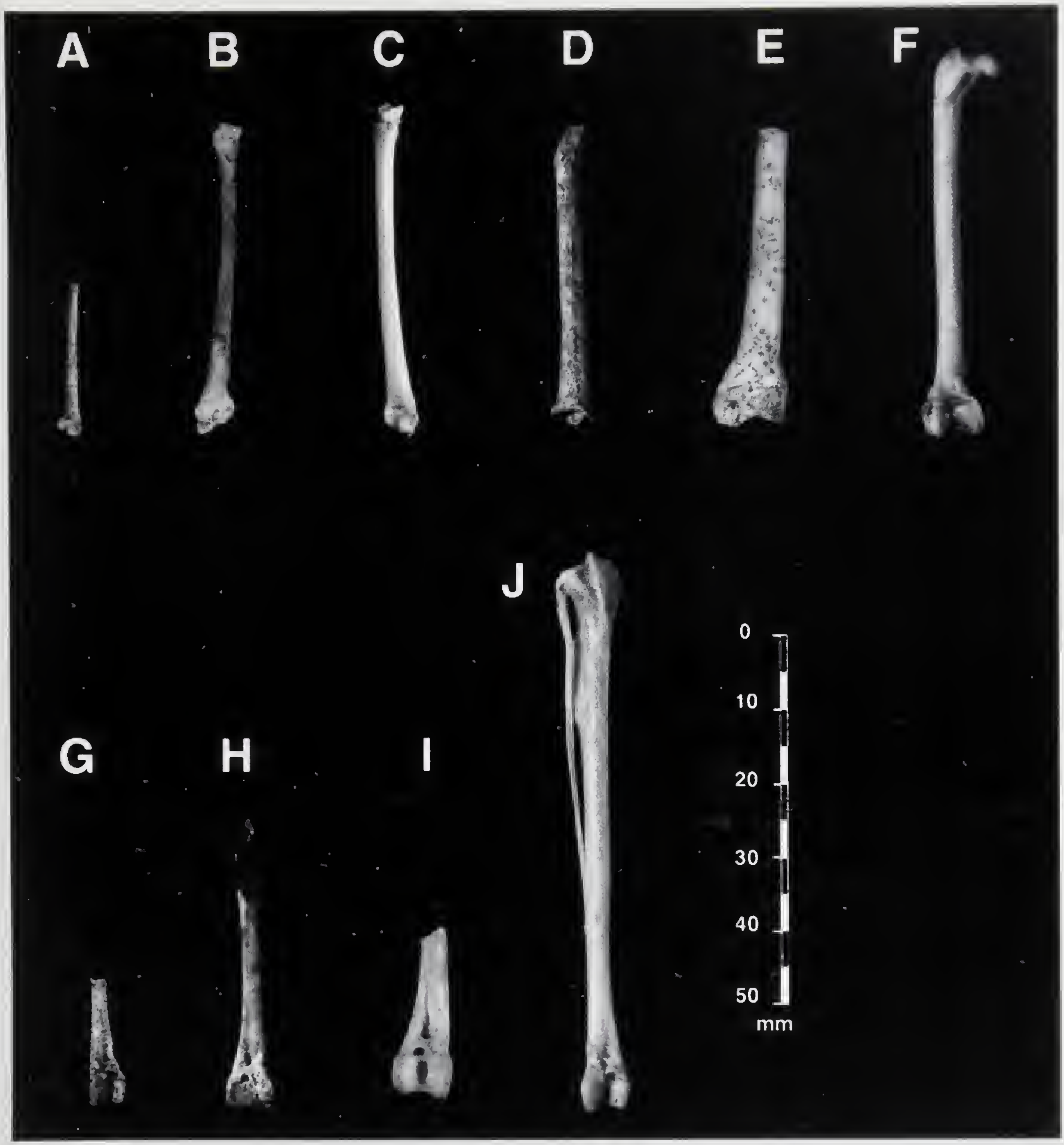

FIG. 12. The ulna in ventral aspect (A–C), femur in ventral aspect (D–F), and tibiotarsus in dorsal aspect (G–J) of *Gallirallus*. A, D, G. *G. huiatua*, MNZ S37709–S37711. H. *G. ripleyi*, USNM 402895. B, E, I. *G.* undescribed sp., UF 51734, 52518, 51729 ('Eua, Tonga). C, F, J. *G. philippensis*, MNZ 25267.

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TABLE 5. Measurements (in mm) of the ulna, femur, tibiotarsus, and tarsometatarsus of *Gallirallus,* with mean, range, and sample size.

	G. huiatua Niue (SU)	*G. ripleyi* Mangaia (SU)	*G.* undescribed sp. 'Eua (SU)	*G. philippensis* Tonga, Samoa (3M, 2F)
ULNA				
A. Proximal depth	3.7 1	—	5.5 1	4.7 4.1–5.1 5
B. Width of midshaft	1.9 1	1.8 1	3.2 3.1–3.3 2	2.8 2.4–3.1 5
C. Depth of midshaft	1.5 1	1.3 1	2.4 2.4 2	2.3 2.0–2.5 5
C/A	0.41	—	0.44	0.50 0.48–0.52 5
C (ulna)/C (femur)	0.41	0.39	0.54	0.63 0.61–0.67 5
FEMUR				
A. Length of shaft	29.6 1	25.5 1	38.5 1	34.4 29.6–38.2 5
B. Width of midshaft	3.5 1	2.9 1	4.4 4.2–4.5 3	3.7 3.1–4.1 5
C. Depth of midshaft	3.7 1	3.3 1	4.4 4.1–4.7 3	3.7 3.3–4.1 5
D. Least depth of distal shaft	3.4 1	3.4 1	4.5 4.2–4.8 3	3.6 3.2–4.0 5
B/A	0.12	0.11	0.12	0.11 0.10–0.11 5
C/A	0.12	0.13	0.12	0.11 0.10–0.11 5
D/A	0.11	0.13	0.12	0.11 0.10–0.11 5
TIBIOTARSUS				
Least width of shaft	2.5 1	2.7 2.3–2.9 5	3.8 1	3.3 2.9–3.6 5
Least depth of shaft	2.4 1	2.5 2.4–2.7 5	3.2 1	2.9 2.6–3.2 5
Distal width	5.5 1	6.3 1	8.0 1	6.4 5.5–7.2 5

TABLE 5. CONTINUED.

	G. huiatua Niue (SU)	*G. ripleyi* Mangaia (SU)	*G.* undescribed sp. ‘Eua (SU)	*G. philippensis* Tonga, Samoa (3M, 2F)
Depth of inner condyle	5.8 est	6.0	7.8	6.8
				6.2–7.2
	1	1	1	5
Depth of outer condyle	5.7 est	5.9	7.3	6.5
		5.6–6.2		6.0–7.0
	1	2	1	5
TARSOMETATARSUS				
Total length	39.5 est	32.9	45.1	45.0
				40.0–49.9
	1	1	1	4
Length of shaft	30.9	25.0	33.6	37.3
				30.9–39.6
	1	1	1	5
Proximal width	5.6 est	5.7	8.7	6.7
				5.8–7.4
	1	1	1	5
Proximal depth	6.4	5.8	8.8	7.0
				6.5–7.4
	1	1	1	5
Least width of shaft	2.5	3.1	4.5	3.1
		3.1		2.7–3.4
	1	2	1	5
Least depth of shaft	2.2	2.1	2.9	2.6
		2.0–2.2	2.7–3.1	2.3–2.8
	1	3	2	4
Distal width	6.3	6.2	8.3	6.7
		6.1–6.3	7.8–8.8	6.2–7.2
	1	3	2	4

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ESTABLISHMENT AND PERSISTENCE OF MASS HIERARCHIES IN BROODS OF THE BROWN PELICAN

MARK A. SHIELDS[1,2]

ABSTRACT.—I investigated the roles of intraclutch variation in egg volume and hatching asynchrony in the establishment of mass hierarchies in broods of the Brown Pelican (*Pelecanus occidentalis*). The second egg averaged 2.6% larger than the first and 1.9% larger than the third. In unmanipulated control broods, first eggs hatched an average of 25 h before second eggs, which hatched 40 h before third eggs. On the day the last egg hatched, first chicks averaged 16% heavier than second chicks and 30% heavier than third chicks. Although chick mass at hatching was strongly correlated with egg volume, differences in mass within broods were almost entirely the result of hatching asynchrony. In broods in which I experimentally reduced hatching intervals, initial nestling mass differences were significantly smaller and strongly correlated with differences in egg volume but not with hatching asynchrony. Intrabrood mass differences remained lower in experimental than control broods throughout the first 2 weeks of the nestling period. Furthermore, mass ranks established at hatching were less likely to persist through this period in experimentally synchronized broods than in asynchronous controls. These results indicate that hatching asynchrony promotes the establishment of a more stable size hierarchy. However, the adaptive significance of nestling size hierarchies in Brown Pelicans remains unresolved. *Received 10 June 1999, accepted 5 Dec. 1999.*

Nestlings within broods of altricial birds often differ considerably in size at hatching (Stokland and Amundsen 1988, Ohlsson and Smith 1994, Viñuela 1996). These initial size differences might result in competitive asymmetries that influence subsequent nestling growth and survival (Ploger and Mock 1986, Bryant and Tatner 1990, Pinson and Drummond 1993). Establishment of a size-based feeding hierarchy within the brood is often regarded as a parental strategy for coping with unpredictable food supplies (the brood reduction hypothesis; Lack 1947, 1954; see Stoleson and Beissinger 1995 for alternative hypotheses). Parents may create a size hierarchy by beginning incubation before the last egg is laid, thereby inducing the clutch to hatch asynchronously (Clark and Wilson 1981, Stoleson and Beissinger 1995). Hatching asynchrony provides first hatched chicks a headstart by giving them the opportunity to feed and grow before their siblings have hatched (Stokland and Amundsen 1988, Magrath 1992, Viñuela 1996). Because hatchling size often is strongly correlated with egg size (Williams 1994), parents adopting a brood-reduction strategy also are expected to lay a relatively small final egg to enhance the effect of hatching asynchrony on nestling size disparities (Slagsvold et al. 1984).

In this paper, I characterize nestling mass differences within broods of the Brown Pelican (*Pelecanus occidentalis*), a species purported to practice adaptive brood reduction (Pinson and Drummond 1993; but see Ploger 1997). My main objectives are to (1) assess the relative contributions of hatching asynchrony and intraclutch variation in egg size to the establishment of initial nestling mass hierarchies, and (2) determine if initial mass hierarchies persist through the early nestling period. A basic premise of the brood reduction hypothesis is that stable size hierarchies will not develop in synchronously hatched broods (Lack 1947, 1954). I test this premise by comparing the magnitude and persistence of nestling mass disparities between naturally asynchronous and experimentally synchronized broods.

METHODS

Study area and field procedures.—I studied a ground nesting population of Brown Pelicans on two small (5 ha) islands in the Cape Fear River estuary, southeastern North Carolina. In 1992 I worked in a colony of about 400 breeding pairs on South Pelican Island (33° 56′ N, 77° 59′ W). In 1993 I worked in a colony of about 200 pairs on Ferry Slip Island (33° 58′ N, 77° 57′ W). I studied 200 nests in 1992 and 100

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TABLE 1. Frequency of occurrence, estimated duration, and estimated time until hatching completed for six stages of hatching in Brown Pelican eggs.

Hatching stage	*n*	Frequency (%)	Duration (h)	Time (h) until hatching
(1) No external sign visible, but embryonic vocalizations heard	44	5.0	2	32
(2) Small star-shaped fracture in shell	139	15.8	5	29
(3) Elevated star-shaped fracture	62	7.0	2	25
(4) Hole pipped in egg	531	60.3	20	14
(5) Shell cut widthwise from pipped hole	62	7.0	2	3
(6) Shell cap removed or chick free from shell but with membranes still adhering to it	43	4.9	2	1

nests in 1993. I visited nests once each morning, weather permitting, during the laying period (early to mid-April) to mark eggs and determine the order of laying. On the day an egg was first observed, I measured its length (L) and maximum breadth (B) to the nearest 0.01 cm with a Vernier caliper. I then calculated the volume (V; ml) of each egg according to Hoyt's (1979) equation: $V = 0.51 \times L \times B^2$.

When egg laying was completed, I reduced the frequency of visits to 2–4 per week until a few days before the end of the incubation period. At this time I resumed daily visits, weather permitting, to record the time of hatching of each egg. Upon hatching, each chick in a brood was uniquely marked with a colored plastic leg band and weighed to the nearest 0.1 g on a portable electronic scale. All chicks in a brood were weighed on the day the last chick hatched (brood day 0) and again 7 and 14 days later (brood days 7 and 14, respectively). When nestling mass exceeded the 300 g capacity of the electronic scale, I used spring scales with capacities of 500 g, 1 kg, or 2.5 kg to measure mass to the nearest 5, 10, or 50 g, respectively. Measurements of most nestlings had to be terminated after brood day 14 to avoid undue disturbance of the increasingly mobile chicks. My frequent visits prior to this time had no discernable adverse effect on nesting success. In fact, nest survival in the sample reported here was slightly higher than in another sample of nests I visited only 3 times during the same period in 1992 (unpubl. data).

Quantification of hatching time.—I quantified the degree of hatching asynchrony between two chicks by calculating the difference in their hatching times. I estimated the time of hatching of each chick to the nearest hour using the method of Stokland and Amundsen (1988) and Viñuela (1996). With this method, the duration of each distinct stage of the hatching process is estimated (Table 1) and the time of hatching of a chick is determined based on the hatching stage in which it was last observed. The duration of each hatching stage was estimated to the nearest hour by multiplying its relative frequency by the total duration of hatching, which I estimated to be 33 h (Shields 1998). The duration of stage 1 may have been underestimated because this stage could be detected only when embryos vocalized, which they did intermittently. For all other stages there was a visible external indicator; consequently, these stages were less likely to be undetected.

I estimated the time of hatching of each egg as follows. When a hatching stage was observed only on the day before a chick was first seen, I assumed that the observation occurred at the midpoint of that hatching stage (Stokland and Amundsen 1988, Viñuela 1996). Thus, the time until hatching was calculated as half the duration of the observed hatching stage plus the sum of the durations of all subsequent stages. When a hatching stage was observed on each of the two days immediately preceding the first observation of a chick, I assumed that the observation of the shorter of the two stages occurred at the midpoint of that stage. This reduced potential errors in estimated hatching times because the midpoint should be closer to the actual time of observation in the shorter than in the longer of the two observed stages.

Manipulation of hatching asynchrony.—I experimentally synchronized hatching in 15 broods in 1992 and 36 broods in 1993 by swapping eggs at the same hatching stage (n = 45 broods) or chicks less than 24 h old (n = 6 broods) among triads of nests. On any given day, the number of nests in which eggs were at the same stage of hatching was limited. Consequently, I made no attempt to match eggs or chicks by size when creating these broods. I also altered hatching patterns in another 36 broods in 1992 by removing the first and second eggs on the days they were laid and replacing them with surrogate eggs. First and second eggs were held at ambient conditions on site until the morning the third egg was laid, at which time they were returned to their original nest (Shields 1998). This treatment was designed to synchronize hatching by delaying the onset of incubation until clutch completion.

The two groups in which I manipulated hatching asynchrony are referred to as experimental broods. Broods in which hatching was unaltered are designated as control broods. I assessed the effect of experimental treatments on hatching asynchrony by comparing mean intervals between hatching of first and last chicks in experimental and control broods using a two-tailed t-test. Only broods of three, the modal brood size at hatching, were included in this study. Because of the failure of some eggs in a clutch to hatch, especially those whose incubation was experimentally delayed (Shields 1998), and incomplete data on some that hatched, only 53 experimental and 90 control broods could be used for analysis.

Initial nestling mass differences.—I quantified initial nestling mass disparities in each control brood by calculating the differences in mass among siblings in relation to laying order (first − second, second − third, and first − third) on the day the last chick hatched (brood day 0). To evaluate the influence of egg size on these mass differences, I first tested for within-clutch differences in egg size by comparing the mean volumes of all three eggs. Because eggs within a clutch are not independent sampling units, I used a randomized block design to analyze these data. Clutch was a random blocking factor and laying order a fixed treatment factor in a mixed model two-way ANOVA without replication (Zar 1996). Pairwise comparisons of means were made using the Tukey multiple comparison test. I then used simple linear regression to quantify the relationship between egg volume (independent variable) and nestling mass at hatching (dependent variable). Only data from recently hatched chicks (hatching stage 6, Table 1) were included in this analysis. Next, I estimated the hatching mass of all chicks in control broods using this regression. Finally, I compared observed mass differences between siblings to those calculated from the regression to determine the contribution of egg volume to initial nestling mass differences.

I assumed that any mass disparity between siblings that could not be attributed to a difference in egg volume was due to nestling growth during the hatching period. Therefore, I calculated the effect of hatching asynchrony on the establishment of mass disparities by subtracting the mass differences due to egg volume from the mass differences observed on brood day 0. I compared the mass differences due to hatching asynchrony within broods using a two-tailed paired *t*-test. I further investigated the relationship between hatching asynchrony and growth of first and second chicks by regressing the change in chick mass (mass on brood day 0 − estimated hatching mass) on chick age (h) when measured on brood day 0.

The above methods could not be applied to experimental clutches because most consisted of three eggs of the same laying order obtained from three different nests. Instead, I quantified the extent of nestling mass disparities on brood day 0 by calculating the relative difference in nestling mass, defined as the difference in mass between the largest and smallest chicks and expressed as a percentage of the mean mass of all three chicks in the brood on that day (Bryant 1978). To assess how variation in egg volume contributed to these mass differences, I calculated the relative difference in egg volume as the difference in volume between the eggs from which the largest and smallest chicks on brood day 0 hatched, expressed as a percentage of the mean volume of the clutch (modified from Bryant 1978). Hatching asynchrony was calculated as the difference in hatching times between the largest and smallest chicks on brood day 0. For comparative purposes, I also calculated these variables for control broods. I used correlation analyses to assess the influence of relative difference in egg volume and hatching asynchrony on relative difference in nestling mass. Control and experimental broods were analyzed separately. To evaluate the effect that using eggs from three different clutches to create most experimental nests had on egg size variation, I compared mean relative difference in egg volume between control and experimental broods using a two-tailed *t*-test.

Maintenance of mass differences.—Because the size of a nestling relative to its siblings, rather than its absolute size, determined its position in the brood hierarchy (Bryant 1978), I used relative measures to quantify within-brood variation in mass as chicks grew during the first 2 weeks of the nestling period. I evaluated the persistence of intrabrood mass disparities by comparing the magnitudes of relative difference in nestling mass on brood days 0, 7, and 14. Only broods in which all three chicks survived to brood day 14 were used in this analysis. Because measurements obtained on the same brood at three different times are not independent, I used a repeated measures ANOVA to analyze these data. Treatment means were compared using the Tukey multiple comparison test. Control and experimental broods were analyzed separately.

The brood reduction hypothesis predicts that mass differences will be smaller in synchronous broods than in asynchronous ones. I tested this prediction by comparing mean relative difference in nestling mass between experimental and control broods on each of the three brood days using two-tailed *t*-tests. To maintain an overall Type I error rate of 0.05 for these comparisons, I adjusted the significance level of each test to 0.017 using the Bonferroni method (Bart et al. 1998).

Calculations of relative difference in nestling mass on brood days 7 and 14 were based on the difference in mass between the largest and smallest chicks on those days. This variable represented the maximum difference in mass within the brood without taking into account the identities of the largest and smallest chicks. Therefore, it cannot be used to evaluate the stability of mass hierarchies because the largest and smallest chicks in a brood in one week may not be the largest and smallest, respectively, the next week. To measure the stability of mass hierarchies, I ranked each chick in a brood according to its relative mass and then determined whether these mass-ranks remained the same or changed from one week to the next. The proportion of broods in which mass-ranks remained unchanged was used as the measure of stability. According to the brood reduction hypothesis, stable mass hierarchies will develop in asynchronous broods, but not in synchronous broods. I tested this premise by comparing the proportions of control and experimental broods in which mass-ranks did not change between brood days 0 and 7 and between brood days 7 and 14.

I used *G*-tests of independence with Yates' correction for continuity to analyze these data.

Data for both years exhibited similar trends and were pooled for all analyses to increase sample size and statistical power. Statistical tests were performed using NCSS for Windows (version 6.0; Hintze 1996). Results are presented as means ± SE.

RESULTS

Initial mass differences in control broods.—Eggs generally hatched in the order in which they were laid, with first eggs hatching 25 ± 1.4 h (range 4–52 h) before second eggs, which in turn hatched 40 ± 1.4 h (range 8–85 h) before third eggs ($n = 90$ clutches). The only exceptions were one nest in which the second laid egg hatched first and three nests in which the first and second laid eggs hatched at the same time. Third laid eggs always hatched last. On the day the third egg hatched, mean masses of chicks from first, second, and third laid eggs were 104.8 ± 2.8 g, 88.0 ± 1.4 g, and 73.9 ± 0.7 g, respectively.

Egg volume varied significantly with respect to laying order ($F_{2,178} = 13.27$, $P < 0.001$). First and third eggs had similar volumes (97.5 ± 0.8 ml and 98.2 ± 0.9 ml, respectively; Tukey test: $q = 1.98$, 178 df, $P > 0.05$), but both were significantly smaller than second eggs (100.1 ± 0.8 ml; Tukey test: first vs second: $q = 7.05$, 178 df, $P < 0.001$; third vs second: $q = 5.07$, 178 df, $P < 0.005$). Regression of chick mass at hatching (y) on egg volume (x) revealed that a difference of 1.0 ml in volume resulted in a 0.8 g difference in hatchling mass ($y = -3.2 + 0.8x$, $r^2 = 0.93$, $n = 40$, $P < 0.001$). Thus, on average, the larger volume of second eggs reduced the initial mass difference between first and second chicks by about 2 g and increased the difference between second and third chicks by 1.5 g (Table 2). Consequently, hatching asynchrony generally accounted for all of the mass difference observed on brood day 0 between first and second chicks and between first and third chicks, and 89% of the difference between second and third chicks. Relative difference in nestling mass on brood day 0 was strongly correlated with the hatching interval between the largest (usually first) and smallest (usually third) chicks ($r = 0.47$, 88 df, $P < 0.001$), but not with relative difference in egg volume ($r = 0.19$, 88 df, $P > 0.05$).

TABLE 2. Effects of egg volume and hatching asynchrony on initial mass differences (g) between siblings in control broods ($n = 90$) of the Brown Pelican.

Mass difference	First and second chicks			Second and third chicks			First and third chicks		
	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range
Observed	16.8	2.1	−21.7 to 88.2	14.0	1.2	−7.4 to 42.8	30.8	2.6	−26.6 to 109.1
Attributed to egg volume	−2.1	0.4	−10.4 to 7.4	1.5	0.4	−9.7 to 11.8	−0.6	0.5	−13.7 to 12.9
Attributed to hatching asynchrony	18.9	2.1	−15.1 to 90.5	12.5	1.1	−6.9 to 40.7	31.4	2.5	−19.9 to 112.1

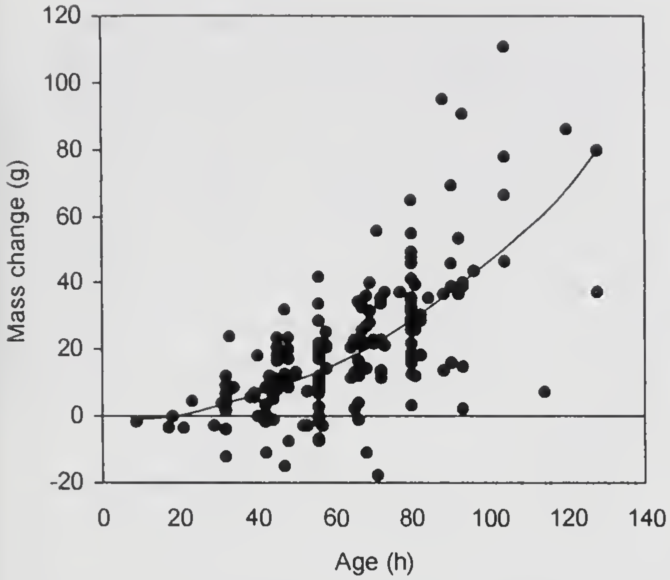

FIG. 1. Relationship between age and change in mass during the hatching period (mass on brood day 0 − estimated hatching mass) for first and second chicks in 90 control broods of the Brown Pelican. Regression equation: $y = -5.9 + 0.2x + 0.004x^2$, $R^2 = 0.47$.

Growth of first and second chicks was slow during the first 1–2 days after hatching but increased more rapidly over the next 2–3 days (Fig. 1). Thus, by the time third chicks hatched, first chicks were growing more rapidly than their second siblings. Consequently, mass disparities caused by hatching asynchrony were greater between first and second chicks than between second and third chicks (paired *t*-test: $t = 2.83$, 89 df, $P < 0.01$; Table 2), even though first-to-second hatching intervals were shorter.

Initial mass differences in experimental broods.—Swapping eggs or chicks among some nests and delaying the onset of incubation in others significantly reduced the interval between hatching of first and last chicks in these experimental broods relative to control broods (14 ± 1.6 h, $n = 53$ vs 64 ± 2.0 h, $n = 90$; *t* with unequal variances = −19.60, 140 df, $P < 0.001$). Relative difference in nestling mass on brood day 0 was not significantly correlated with hatching asynchrony ($r = -0.12$, 51 df, $P > 0.05$). However, it was strongly correlated with relative difference in egg volume ($r = 0.74$, 51 df, $P < 0.001$), which was significantly larger in experimental than control clutches (7.9 ± 1.1% vs 0.6 ± 0.6%; *t* with unequal variances = 5.98, 87.5 df, $P < 0.001$).

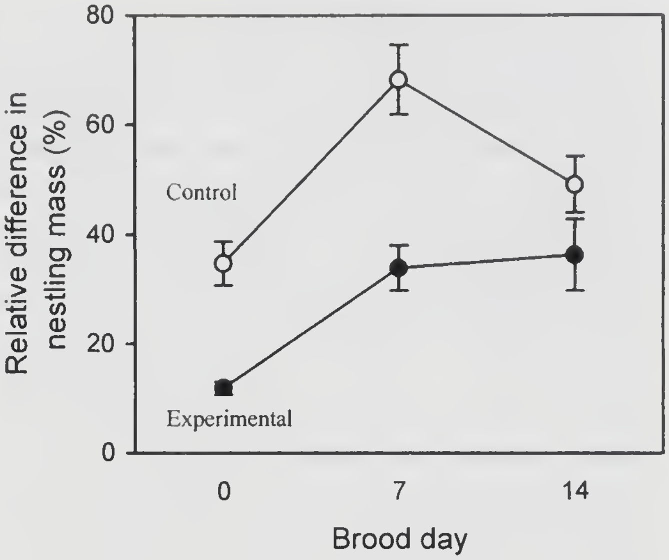

FIG. 2. Relative difference in nestling mass ($\bar{x}$ ± SE) for 23 control and 27 experimental broods of the Brown Pelican during the first 2 weeks after hatching.

Persistence of mass differences.—Relative difference in nestling mass varied significantly over time in both control ($F_{2,44} = 41.35$, $P < 0.001$) and experimental broods ($F_{2,52} = 12.90$, $P < 0.001$; Fig. 2). Mean relative difference in nestling mass was significantly smaller on brood day 0 than on brood days 7 and 14 in both groups (Tukey test: control: 0 vs 7: $q = 12.82$, 44 df, $P < 0.001$; 0 vs 14: $q = 5.50$, 44 df, $P < 0.005$; 7 vs 14: $q = 7.34$, 44 df, $P < 0.001$; experimental: 0 vs 7: $q = 5.88$, 52 df, $P < 0.001$; 0 vs 14: $q = 6.52$, 52 df, $P < 0.001$; 7 vs 14: $q = 0.64$, 52 df, $P > 0.05$). However, relative difference in nestling mass remained lower in experimental broods throughout the first two weeks of the nestling period (Fig. 2). Differences between the 27 experimental and 23 control broods were highly significant on brood days 0 (*t* with unequal variances = −5.84, 26.3 df, $P < 0.001$) and 7 ($t = -4.70$, 48 df, $P = 0.001$), but not on brood day 14 ($t = -1.50$, 48 df, $P > 0.05$).

Stability of hierarchies.—Mass hierarchies established on brood day 0 were more likely to remain unchanged through brood day 7 in control than experimental broods (19 of 23 vs 8 of 27; $G = 12.62$, 1 df, $P < 0.001$). However, mass-ranks on brood day 7 were just as likely to remain unchanged through brood day 14 in experimental as control broods (22 of 27 vs 17 of 23; $G = 0.09$, 1 df, $P > 0.05$).

DISCUSSION

Initial nestling mass disparities within control broods were established primarily by chick growth during the hatching period, which was a function of the degree of hatching asynchrony (Fig. 1). Although hatchling mass was positively correlated with egg volume, the generally larger volume of second eggs lessened the disparity created by hatching asynchrony between first and second chicks by 11% and exaggerated the difference between second and third chicks by a similar amount. Because first and third chicks hatched from eggs of similar size, egg volume had virtually no effect on the large mass differences observed between these chicks (Table 2). In the Shag (*Phalacrocorax aristotelis*), another pelecaniform with similar patterns of egg size variation and hatching asynchrony, initial nestling mass disparities also are almost entirely the result of hatching asynchrony (Stokland and Amundsen 1988). Similarly, egg size variation has a negligible effect on nestling size hierarchies in Blue-eyed Shags (*P. atriceps*; Shaw 1985) and a variety of other asynchronously hatching altricial species in which brood reduction (in the broad sense; Mock 1994) occurs (Magrath 1990, Ohlsson and Smith 1994, Viñuela 1996). Thus, contrary to the suggestion of Slagsvold and coworkers (1984), intraclutch variation in egg size does not appear to be a mechanism by which these brood reducing species facilitate the formation of nestling size hierarchies.

Egg volume had a much stronger influence on initial mass disparities in experimental broods because chicks had little time to grow during the shortened hatching period. This suggests that even in the absence of hatching asynchrony, parents still may be able to produce nestling size hierarchies through intraclutch variation in egg size. However, the importance of egg volume was exaggerated by the experimental procedure. I created most experimental broods using eggs from three different clutches without attempting to maintain the normal degree of intraclutch variation in size. Because egg volume varied more among than within clutches (Shields 1998), this resulted in the mean relative difference in egg volume being an order of magnitude larger in experimental broods than in control broods. Despite this, initial nestling mass differences within experimental broods were both significantly smaller and less likely to result in the formation of stable mass hierarchies than mass disparities produced by hatching asynchrony in control broods. Therefore, intraclutch egg size variation appears to be unimportant to establishment of stable nestling size hierarchies in either synchronous or asynchronous broods of Brown Pelicans, as was reported for Black Kites (*Milvus migrans*; Viñuela 1996).

Differences in the magnitude and stability of nestling mass disparities between control and experimental broods were due to differences in patterns of nestling growth, which were affected by the degree of hatching asynchrony. Growth of Brown Pelican chicks is slow during the first 24–48 h after hatching, but increases in the following days (Fig. 1), ultimately exhibiting a sigmoidal pattern with an inflection point at about 25 days of age (Schreiber 1976). During the first week after hatching, chicks feed almost exclusively by pecking at partially digested fish regurgitated by their parents onto the floor of the nest (Pinson and Drummond 1993). As chicks grow and become more coordinated in their movements, they begin to intercept regurgitated food from their parents' beaks or pouches before it reaches the nest floor (Pinson and Drummond 1993). Brown Pelican chicks are aggressive throughout the early nestling period, often pecking their siblings both during and between feeding bouts (Ploger 1992, Pinson and Drummond 1993).

Asynchronous hatching in control broods created uneven-aged broods. Older chicks, with their more developed motor skills, were better able to direct their pecks at food and their siblings, giving them an initial advantage in competition for food deposited on the nest floor and in the establishment of dominance-subordinance relationships (Pinson and Drummond 1993). This advantage quickly translated into an even larger size disparity than was present at hatching (Fig. 2). The size advantage afforded first hatched chicks by hatching asynchrony was maintained for at least the first 2 weeks after hatching, and probably persisted until chicks reached maximum mass several weeks before fledging (Schreiber 1976, Pinson and Drummond 1993).

Synchronous hatching in experimental broods, on the other hand, resulted in even-aged broods. The small mass differences resulting from variation in egg volume were insufficient to establish stable mass hierarchies, even though egg volume varied more in experimental than control broods. Instead, differences in motor skills probably were more important initially (Viñuela 1996). Even a slight advantage in coordination of movements may have allowed a chick to establish dominance over its brood mates in the first few days after hatching, regardless of its position in the initial mass hierarchy (Osorno and Drummond 1995). This may explain why mass hierarchies were unstable between brood days 0 and 7, but stabilized during the next week. This also might explain why dominance hierarchies often develop in experimentally synchronized broods of other altricial species (Gibbons 1987, Mock and Ploger 1987, Amundsen and Slagsvold 1991).

According to the brood reduction hypothesis (Lack 1947, 1954), the size hierarchy imposed by hatching asynchrony is a parental evolutionary adaptation for allowing the facultative adjustment of brood size to match the food supply. Should food become too scarce to sustain the entire brood, the smallest chick can be quickly eliminated through sibling competition, thus ensuring partial brood success. Rivalry among the more evenly matched siblings in synchronously hatched broods, on the other hand, would jeopardize survival of the entire brood if food was in short supply (Lack 1947). My findings, while not constituting a test of the brood reduction hypothesis, substantiate several of its basic premises. First, asynchronous hatching, which is controlled mainly by parental incubation behavior (Shields 1998), promoted the development of significantly larger intrabrood mass disparities than synchronous hatching. Second, mass hierarchies established at the completion of hatching in asynchronous broods persisted through at least the first 2 weeks of the nestling period, thus allowing time for brood reduction to occur should food become limited. This period coincides with the time when most mortality of last hatched chicks occurs in this species (Ploger 1992, Pinson and Drummond 1993, Shields 1998). A third key premise of the hypothesis, that stable size hierarchies would not develop in synchronously hatched broods, was not unequivocally supported. Mass hierarchies established at the completion of hatching in the more synchronous experimental broods usually did not remain stable through the first week after hatching. Hierarchies generally stabilized after this time, although mass differences within broods tended to be of lesser magnitude than those in asynchronous broods.

These results suggest that adaptive brood reduction, should it become necessary, could be effected earlier and thereby more efficiently in asynchronous broods than in synchronous broods (Husby 1986, Gibbons 1987, Magrath 1989). However, the potential for unnecessary (maladaptive) deaths of smaller, less competitive siblings also may be higher in asynchronous broods (Clark and Wilson 1981, Stouffer and Power 1990, Pijanowski 1992). Last hatched chicks in Brown Pelican broods often succumb to starvation (Schreiber 1976) or siblicidal attacks (Ploger 1992, Pinson and Drummond 1993). If this mortality represents the adaptive adjustment of brood size when food is scarce, surviving siblings should benefit by receiving the food that would have gone to the third chick had it lived (O'Connor 1978, Stinson 1979), and asynchronous broods should produce more fledglings than synchronous broods (Lack 1947, 1954). Contrary to these predictions, Brown Pelicans deliver less food to their broods after brood reduction than before (Ploger 1997), and asynchronous broods produce fewer fledglings than synchronous broods in poor food years (Shields 1998). These findings, like those of most studies of the adaptive significance of hatching asynchrony (reviewed by Stoleson and Beissinger 1995), do not support the brood reduction hypothesis. Instead, they suggest that mortality of last hatched chicks is a cost, not a benefit, of the size hierarchy imposed by hatching asynchrony in Brown Pelicans. However, size hierarchies may still be adaptive if the reduction in parental effort following brood reduction results in an increase in adult survival and future fecundity (Mock and Forbes 1994). Whether such long-term gains can compensate for the short-term loss of reproduction resulting from brood reduction remains to be determined.

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BREEDING BIOLOGY AND NEST SITE CHARACTERISTICS OF THE BICOLORED HAWK IN GUATEMALA

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ABSTRACT.—We studied the breeding biology of the Bicolored Hawk (*Accipiter bicolor*) in the forest of Tikal National Park of northeastern Guatemala from 1991 to 1994. Bicolored Hawks are year-round residents and establish nesting territories during the breeding season, which coincides with the late dry season and beginning of the wet season. Nest building and courtship spanned 92 days. We documented 17 nesting attempts from February to July 1991–1994. Egg-laying began in April and May, with 36 eggs laid in 15 nests for an average clutch size of 2.4 (range 1–3 eggs). We documented one renesting after failure of the first clutch. Incubation was approximately 35 days (n = 5 clutches). Young hatched asynchronously with a light pinkish natal down. Of 36 eggs laid, 64% hatched. Nearly all hatching occurred during May except one renesting, from which one young hatched on 26 June 1994. Young departed from the nest tree at 30–36 days of age and 100% of the nestlings fledged; thus a total of 1.4 young fledged per breeding attempt and overall nest success was 76%. Most reproductive losses occurred during the incubation period. We found addled eggs in 2 nests and egg predation and nestling predation at 1 nest each. Bicolored Hawk nests averaged 22 m above the ground in living trees 75 cm in diameter. All nests were stick nests, averaging 51 × 44 cm exterior diameter, 26 cm exterior depth, and 3.6 cm interior depth. The Bicolored Hawk diet of 173 identified prey was composed almost exclusively of birds (95%) with relatively few mammals (3%) or reptiles (2%) taken. *Received 3 June 1999, accepted 26 Jan. 2000.*

Among Neotropical birds, raptors are one of the least studied groups and relatively little is known about their breeding biology (Thiollay 1985, Bierregaard 1995). Raptors in tropical environments tend to have longer breeding seasons and lower reproductive rates than their temperate counterparts (Newton 1979, Mader 1982, Delannoy and Cruz 1988, Thorstrom 1993). Tropical raptors are also known to lay replacement clutches after losing eggs or young, which rarely occurs in temperate areas (Newton 1979, Mader 1982, Delannoy and Cruz 1988).

The widespread genus *Accipiter* includes seven small to medium-sized hawks confined to the mainland Neotropics. One widely distributed Neotropical accipiter is the Bicolored Hawk (*Accipiter bicolor*), member of a superspecies that includes the Cooper's Hawk (*A. cooperi*), Gundlach's Hawk (*A. gundlachi*), and Chilean Hawk (*A. chilensis*: del Hoyo et al. 1994).

The Bicolored Hawk is widespread but rarely observed, ranging from northern Argentina to southern Mexico. It mainly inhabits lowland and subtropical forests but also reaches the lower limit of the temperate zone around 2500 m in the Andes (del Hoyo 1994, Fjeldså and Krabbe 1990). During raptor surveys in and around Tikal National Park, a lowland tropical forest of northeastern Guatemala, this species was rarely detected in visual or aural censuses (Whitacre et al. 1991, Jones and Sutter 1992). Smithe (1966) reported Bicolored Hawks as "uncommon but not rare" at Tikal National Park, while Beavers (1992) coded it as rare.

Little is known about the breeding biology of the Bicolored Hawk. Unlike Temperate raptors, it is very difficult to detect because it is secretive, inconspicuous, its vocalizations are weak even during the breeding period, and pairs do not appear to perform courtship flights over the nest area (Palmer 1988). Mader (1981) reported one successful breeding attempt that fledged two young and one nest built and then abandoned, both during the wet season (April and May) in Venezuela. Our study summarizes information collected during four years on breeding biology, behavior, and nests of this inconspicuous forest raptor.

STUDY AREA AND METHODS

This study was conducted in Tikal National Park (17° 13′ N, 89° 36′ W) which encompassed 576 km^2. This park is in a lowland, dry, semi-deciduous, tropical forest with an annual mean rainfall of 1348 mm (based on 1989–1992 data). Several forest types, which occur

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along topographical drainage, soil type, and moisture gradients, have been described for the park (Schulze and Whitacre 1999). Two extremes of this continuum are upland or high-ground forests (tall, semi-evergreen forests on well-drained shallow soils) and "bajo" forests (low in stature, with open canopy and dense understory, occurring in low-lying sites of deep clay-rich soils, subject to seasonal flooding and drought). Between these two readily distinguishable forest types is a transitional zone at the base of hills or on slopes from uplands to low lying basins.

Paired birds and nests were located opportunistically during foot searches for forest-falcons and other potentially nesting raptors. One nest was located from a trapped and radio-tagged male. Nest observations were made from the ground and from tree platforms with 8× and 10× binoculars at distances of 35–50 m. We observed each nest site 5–6 hours per observation period and rotated between mornings and afternoons every three to four days. Nest measurements were taken on accessible nests. Nest height was measured in plumb-line distance from the nest to ground level and nest tree diameter was measured at breast height. The incubation period was calculated as the time (days) from laying of last egg (after clutch completion) to hatching of the last egg. We measured egg dimensions to the nearest 0.1 mm with vernier calipers and determined egg mass and body mass of adults with 100 g and 500 g Pesola spring scales to the nearest 1 g and 5 g, respectively. Bicolored Hawks were trapped with bal-chatris and a noose carpet placed near or on the nest during incubation (Newton 1986, Thorstrom 1996). Six birds were color banded for identification.

For our analyses reproductive variables were defined as territorial pair-years (territories where pairs bred or maintained a territory but did not breed; several nests were constructed but no eggs were laid), nesting (breeding) attempt (nests that contained at least one egg), eggs laid (number of observable eggs laid in accessible nests), mean clutch size (number of observable eggs laid per nesting attempt), eggs hatched (number of eggs hatched), young fledged (number of young surviving to fledging), productivity (number of young fledged per nesting attempt), overall productivity (number of young fledged per territorial pair), and nest success (number of total nesting attempts that fledged at least one young).

Breeding density was determined by two methods. We calculated the mean neighbor distance between nests following Selås (1998) and determined the radius from this measurement. The area of a nesting territory was calculated as $A = \pi r^2 \times 1.158$, where 1.158 is a constant that included the area of non-overlap between neighboring territories (Brown 1975). Breeding density was also calculated from the polygon area that enclosed all nests located and might include unused habitat. The polygon was produced by connecting the outermost nests and then extending the sides by half the mean minimum internest distance (Berkelman 1996). The demarcated area was calculated by CAMRIS GIS (Ecological Consulting, Inc., Portland, Oregon). Except where stated, measures give are means ± SD.

RESULTS

We located 3 nest sites in 1991, 2 in 1992, 1 in 1993, and 1 in 1994 for a total of 7 nesting territories.

Courtship behavior and nest building.—Courtship activities occurred from February to April. No territorial or aerial flights were observed in this species. Courtship behavior consisted of vocalizations, nest building activities, courtship feedings, copulations, and nest defense. Both adults took part in nest construction. The earliest nest building activity was observed on 5 February 1992. In 1991, during 100 h of observation at three nests, we observed deliveries of 81 dry sticks with males contributing 41 (50.6%) and female 40 (49.4%). Most nest building and copulations occurred 06:00–07:00. The earliest copulation was observed on 28 February 1992, approximately 5 weeks before egg laying. Copulations usually occurred after courtship feedings, and occasionally after nest building activities. From 05:30 to 06:30, one pair was observed copulating 3 times. Nest building and courtship spanned 92 days (5 February to 8 May) and peaked in mid-March.

Nest characteristics.—Nests were built in trees on single or forked branches or on hanging vines. Birds collected dry sticks and twigs from trees within 20–50 m of the nest site. Several nests contained dried leaves as nesting material in the nest cup. Nearly all pairs built new nests every year and the average distance between alternate nests in a given territory in successive years was 94 ± 57 m (range 30–200 m, $n = 10$). Two nests were used by the same banded pairs for 2 years (1992, 1993) and one for 3 consective years (1991–1993). In 1994, one pair reconstructed and occupied the nest of a Crane Hawk (*Geranospiza cearulescens*) built in 1993. We documented only one renesting effort after first clutch loss and that pair constructed a new nest in 3 weeks from 5–23 May 1994.

Bicolored Hawk nests averaged 21.7 m above the ground in live trees averaging 74.6 cm dbh (Table 1). Thirteen nests were supported by branches and two were supported by hanging vines. Forty percent ($n = 6$) of nest trees were situated in bajo forest, 53.3%

TABLE 1. Bicolored Hawk nest site characteristics.

Nest site characteristics	Mean	SD	Range	*n*
Nest height (m)	21.7	2.3	17.2–27	15
Nest tree diameter (cm)	74.6	16.9	58.2–124	15
Nest width (cm)	43.6	12.8	15–63	12
Nest length (cm)	51.3	15.8	30–97	15
Nest depth exterior (cm)	26.5	11.7	12–30	14
Nest depth interior (cm)	3.6	2.1	2–9	15
Nest support branch diameter (cm)	9.4	4.8	4–15	11
Nest distance from trunk (m)	3.5	3.7	0–9	11

(*n* = 8) in transitional forest, and 6.7% (*n* = 1) in upland forests. Fifteen of 19 nests were constructed in different trees of 6 species: 33.3% (5) were in *Brosimum alicastrum,* 26.7% (4) in *Swietenia macrophylla,* 13.3% (2) in *Vitex gaumeri,* 13.3% (2) in *Lonchocarpus castilloi,* 6.7% (1) in *Pouteria amygdalina,* and 6.7% (1) in *Manilkara zapota.*

Egg laying, incubation and hatching.—By mid-April, females remained near the nest sites and were mostly inactive. We observed two males (one banded and one unbanded) copulating with the same banded female at one nest site in 1993 prior to egg laying. After egg laying, the unbanded male disappeared, and the banded male attended the female and nest site through a successful breeding attempt. Laying of first clutches spanned 36 days (2 April to 8 May). Earliest recorded laying dates were 4 April 1991, 2 April 1992, 6 April 1993, and 2 April 1994. First clutches averaged 11 April ± 10 days (SD; *n* = 15 clutches) for the four years (range 2 April to 8 May). The most common clutch size was three (*n* = 8), followed by clutches of two (*n* = 5), and there were two one-egg clutches, one of which was a replacement clutch, for a mean clutch size of 2.4 ± 0.7. We suspect that full incubation began when the penultimate egg was laid. Mean dimensions of 14 Bicolored Hawk eggs were 47.1 ± 1.1 mm (44.9–49.0 mm) by 36.5 ± 1.1 mm (35.0–38.6 mm; see Thorstrom and Kiff 1999). Average egg mass was 33.5 ± 3.5 g (28.0–38.0 g, *n* = 14 eggs), 7.1% of the female's body mass (average female body mass was 470 g; *n* = 4), and 21.3% of her mass for a clutch of three eggs.

Females performed most of the incubation, and the males provided food to the female and nestlings. Males gave sharp *kek* calls upon arrival to the nest while females solicited food with a nasal *wreh* vocalization. Occasionally males tried to incubate after delivering food to the female away from the nest, but incubation duration of males ranged from 30 seconds to 5 min at which time females returned to the nest and males moved off. The incubation period from laying to hatching of the penultimate egg was 34 ± 1 days (*n* = 5 clutches). Hatching was asynchronous, spanning 1–3 days. Nearly all hatching occurred during May except for the renesting, from which one young hatched on 26 June 1994 (Table 2). Hatching for all years peaked on 16 May ± 5 days and spanned 14 days (9–23 May, *n* = 10 nests).

Development of young.—One week prior to fledging, young moved around in the nest and onto nearby limbs. Sometimes they were located 3–4 m above and beyond the nest in branches, occasionally fluttering, hopping, and flying back to the nest.

Fledging period and natal dispersal.—Young fledged (took their first flight from the nest tree) 30–36 days after hatching. Males appeared to fledge earlier (30–32 days; *n* = 3) than females (34–36 days; *n* = 2). Fledging spanned nearly 7 weeks, from the first week of June to late July. After fledging, young remained in the nest area and returned to the nest frequently. Adults continued to deliver food to the young during the first few weeks after fledging. When young were capable of handling prey they fed away from the nest and their siblings. Young constantly solicited food and mobbed adults when they entered the nest area.

At one nest site, two telemetered young males probably dispersed on 25 August 1991, when we lost radio contact, 9 weeks after fledging (98 days of age). These two young

TABLE 2. Nestling development and behavior (n = 2 males in 1991).

Age	Measurements (mm)	Weight (g)	Physical characteristics and behavior
Hatch (day 0)		25–28	Light pinkish down, black beaks, white-gray nails and pale yellow ceres
Week 1	Body length 140, wing 90	120	Natal down white, cere yellowish orange and egg tooth disappearing
Week 2	Body length 220, wing 170	200–220	Young with primaries emerging and parasitic fly larvae attached to wing blood feathers
Week 3	Body length 230, wing 225, tail 40	240	
Week 4	Body length 305, wing 153, tail 80		Active in nest calling and moving around
Week 5			Very active and moving outside of the nest on branches

ranged up to 400 m from their nest tree during the post-fledgling period. Two other young were radio-tagged to monitor natal dispersal but they were out of the range of our equipment by four and five weeks, and the lack of roads made coverage of their movements difficult.

Productivity and reproductive success.—Seven territorial pairs were studied for a total of 21 territorial pair-years from 1991 through 1994 (Table 3). In these 21 pair-years, 19 nests were built and 17 nesting attempts were observed (eggs laid). Clutch size was documented for 15 nesting efforts, totaling 36 eggs ($\bar{x}$ = 2.4 eggs). In 10 fully documented nests containing 27 eggs, 20 eggs (74%) hatched and all of the hatched young fledged. In total, 24 young (100%) fledged from 13 breeding attempts, for a productivity of 1.8 young fledged per successful attempt. Overall productivity was 1.1 (24/21) young per territorial pair-year. Nest success for the four years of the study was 76% (13/17).

In the 17 nesting attempts, 3 nest failures occurred during incubation and 1 during the nestling stage. The causes for nest failure were addled eggs (n = 2 nests) and predation (possibly mammalian) on eggs or nestlings (n = 2 nests).

The 7 territorial pairs we documented from 1991 to 1994 fledged 24 young. One pair raised young in each of the four years of the study, producing 33% (n = 8 young) of the total young fledged. This pair used the same nest in three successive years (1991–1993) and moved to another nest site 35 m away in 1994.

Few mortalities were observed in either young or adults. One adult female apparently drowned while attempting to drink from or capture prey near a man-made well. We suspect that overall adult mortality for the Bicolored Hawk is low. For example, one adult female banded in 1991 was still on her territory in 1994. No immature plumaged young was detected on nesting territories.

Breeding density.—Using the mean distance between neighboring nests we calculated that a nesting territory occupied 4.0 km^2 for a total of 23.8 km^2 for six contiguous territories. The six nesting territories were enclosed within a 33.4 km^2 polygon resulting in a breeding territory of 5.5 km^2. This estimate

TABLE 3. Annual reproductive success of Bicolored Hawks during the breeding season 1991 to 1994 at Tikal National Park, Guatemala.

Year	Territorial pair-years	Nesting attempts[a]	Eggs laid (nests)	Mean clutch size	Eggs hatched (%)	Young fledged (%)[b]	Productivity	Overall productivity	Successful nests *n* (%)
1991	3	3	9 (3)	3.0	4 (44)	3 (75)	1.0	1.0	2 (66)
1992	5	5	9 (4)	2.3	8 (89)	10 (100)	2.0	2.0	5 (100)
1993	6	4	8 (3)	2.7	5 (63)	5 (100)	1.3	0.8	3 (75)
1994	7	5	10 (5)	2.0	6 (60)	6 (100)	1.2	1.0	3 (60)
Total	21	17	36 (15)	2.4	23 (64)	24 (100)	1.4	1.1	13 (76)

[a] Number of nests with egg laid.

[b] Two nests were discovered with nestlings before we made an egg count.

also may have included parts of one or two territories for which nests were not found but contained birds.

Food habits.—From 1991–1994, we recorded 272 Bicolored Hawk prey items at Tikal, mainly those brought to nests; 173 were identified at least to class. Birds comprised 95% (164) of identified prey, mammals (bats and rat-sized rodents) 3% (6), and reptiles (lizards) 2% (3). Ninety-nine prey items were unidentified to species; these were often plucked and partly eaten before delivery to the nest, rendering their identification impossible. During the breeding season, adult males were observed taking birds ranging from euphonias (*Euphonia* spp.) and greenlets (*Hylophilus* spp.; 8–16 g) to motmots (*Momotus* spp.; 133 g), while adult females were observed to take ant-tanagers (*Habia* spp.; 31–38 g), toucanets (*Aulacorhynchus* spp.; 150 g) and puffbirds (*Bucco* spp.; 96 g). Wintering Wood Thrushes (*Hylocichla mustelina*; 48 g) and woodcreepers (*Dendrocincla* spp.; 30–80 g) made up the bulk of the species taken by both sexes (weights from Dunning 1993).

DISCUSSION

Breeding cycle.—The courtship and territorial behavior of the Bicolored Hawk appears to differ from other *Accipiter* hawks (Newton 1979, Brown and Amadon 1989). Although soaring has been reported for this species (Fjeldså and Krabbe 1990, del Hoyo et al. 1994), we did not observe soaring flights or aerial displays above the canopy during the breeding season at nest sites or while we conducted raptor surveys from 1988 to 1992 (Whitacre et al. 1992). The birds rarely soared above the forests in northeastern Guatemala, making detection extremely difficult during raptor censuses. In general, they appeared to move through and below the canopy rather than above it. We occasionally sighted individuals sitting on conspicuous perches above the canopy.

At one nest site both members of a pair were banded prior to egg laying in 1991. The female disappeared one week later and a new, unbanded female replaced the marked female. The first banded female was observed nesting the following breeding season (1992) on a neighboring territory, where she successfully fledged three young. This suggests that the pair bond was not firmly established when the first adults were banded in 1991, and that there were unpaired individuals in the population. Unpaired, non-territorial individuals have been documented in other *Accipiter* populations (Newton 1986). In 1993, we recorded one instance of bigamy or extra-pair copulations at one nest site. The intruding male did not appear to have a detrimental effect on the reproductive success of this pair.

The breeding cycle was approximately 188 days from nest building to dispersal of young from their natal areas (February to July). This is comparable to the tropical Puerto Rican Sharp-shinned Hawk (*Accipiter striatus venator*; 184 days), also having a relatively long breeding period (Delannoy and Cruz 1988), which is longer than the Cooper's Hawk in Oregon (132 days) and European Sparrowhawk (*Accipiter nisus*) in Scotland (110 days; Reynolds and Wight 1978, Newton 1986, Delannoy and Cruz 1988). As with the Puerto Rican Sharp-shinned Hawk (Delannoy and Cruz 1988) and the Bicolored Hawk (Mader 1981) in Venezuela, the extended period between occupancy of nesting sites and initiation of laying accounted for the differences in the duration of breeding cycles. The longer breeding period of the Bicolored Hawk compared to the Cooper's Hawk (Millsap 1981, Reynolds and Wight 1978) resulted from early nest building and courtship activity in February, egg laying in April, and a longer fledgling period.

Bicolored Hawks at 17° N latitude in Guatemala constructed nests early in the dry season. Incubation and nestling periods were during the dry season with fledging occurring at the start of the next wet season. In Venezuela, Mader (1981) suggested that raptors might occasionally nest during both wet and dry seasons. Mader (1981) found one pair of Bicolored Hawks constructing a nest in May at the start of the rainy season and fledging young in July. Another pair was observed nest building in May, the start of the rainy season in Venezuela at 6° N (Mader 1981). We suggest that the reason for the variation in timing of the breeding cycle between these two sites is related to local food availability. This difference in the timing of breeding between Guatemala and Venezuela may be caused by the response of different habitats to rains, which might affect the availability of avian prey and ultimately the nesting period of these bird-eating hawks. In Guatemala, young Bicolored Hawks fledged June–July when many species of prey birds also fledge their young.

Food habits.—Reports on diet are few and mostly of hawks taking thrush to pigeon sized birds (Brown and Amadon 1989) and some lizards (Stiles and Skutch 1989). In Venezuela, a Squirrel Cuckoo (*Piaya cayana*; Mader 1981) and a mockingbird (*Mimus gilvus*; Friedmann and Smith 1955) were taken by Bicolored Hawks. The most complete record of prey comes from Peru where 13 birds and 1 squirrel were observed captured or carried as prey (Robinson 1994).

In Guatemala, Bicolored Hawks delivered mainly birds to their nests, but some reptiles and mammals were also recorded as prey. With a 95% avian diet in our sample, the Bicolored Hawk was the preeminent bird-eating specialist at Tikal. Only two other species demonstrated an equivalent reliance on birds: the Bat Falcon (*Falco rufigularis*; Parker 1997), which takes much smaller birds above or within the upper canopy or within openings in the vegetative cover, and the Orange-breasted Falcon (*F. deiroleucus*; Baker 1998), which also takes mainly flying prey above the forest. The two forest-falcon (*Micrastur* spp.) species at Tikal relied substantially less on avian prey, with the large Collared Forest-Falcon (*M. semitorquatus*) taking many mammals. Barred Forest-Falcon (*M. ruficollis*) took many small, arboreal lizards, in addition to avian prey (Thorstrom 1993).

Nest-site characteristics.—Nest trees of Bicolored Hawks were situated in low-canopied bajo forests, transitional forests, and high-ground forests. We speculate that Bicolored Hawks may select these habitat types with their relatively open canopy for easier access to the nest, fewer connections between neighboring trees (more isolated emergents), which would limit movements of arboreal animals, and possibly a lower density of terrestrial predators.

This *Accipiter* is reported to occupy a variety of habitats with no apparent specialization. Bicolored Hawks have been reported to occupy second-growth and even palm savannas with gallery forest, but they appear to be more common in drier or open forests, parkland, forest edges, and rain forests (Fjeldså and Krabbe 1990, del Hoyo et al. 1994). Nest site locations in the bajo and hill base forests possibly provide some protection against nest predators. The low canopied bajo forests appear to limit spider monkey (*Ateles geoffroyi*) activity, possibly reducing the potential for these primates to prey on Bicolored Hawk nests. We observed Bicolored Hawks aggressively defending their nests from spider monkeys and predatory birds, such as Ornate Hawk-Eagles (*Spizaetus ornatus*), Keel-billed Toucans (*Ramphastus sulfuratus*), and Brown Jays (*Corrocoryx murio*).

Breeding density.—Based on home range estimates and breeding densities Bicolored Hawks in Tikal National Park occupied 4.0–5.5 km^2 per territorial pair. Territories were evenly spaced throughout the study area even though Bicolored Hawks were somewhat specific in their nesting requirements for bajo and transitional forests. In a 100 km^2 area, we estimate that the breeding density would range from 18 to 25 territories assuming suitable habitat was available. In French Guinea, Thiollay (1989) estimated that the breeding density for this species was 4 territorial pairs per 100 km^2 or 25 km^2 per pair, 5 times less dense than our estimate. We suspect that a difference in the forest habitat, relatively dry (Tikal National Park) versus wet (French Guiana) tropical forests, may contribute to this large difference. We also speculate that our estimates may reflect the more accurate estimate of the species' breeding density because Thiollay (1989) did not use neighboring territories to estimate Bicolored Hawk densities.

Productivity.—The reproductive output was low during the study with 1.4 young fledged/breeding attempt. Although the reproductive rate was somewhat low, the nesting success was high with an average of 76% of all nesting attempts resulting in successful fledglings. Thus, if a pair of Bicolored Hawks was successful in laying eggs they had a good chance of successfully producing offspring. The Bicolored Hawk population in Tikal appears to be stable and density-dependent.

Production and nesting success was higher for the Bicolored Hawk than for the insular congeneric Puerto Rican Sharp-shinned Hawk (Delannoy and Cruz 1988). The Puerto Rican Sharp-shinned Hawk suffered a higher degree of nest failures from nestling mortality attributed to parasite infestation and desertion of clutches, neither of which were observed in Bicolored Hawks at Tikal National Park. Bicolored Hawks at Tikal National Park were secretive bird-feeding specialists and appeared to be evenly spaced throughout the forest, suggesting that breeding densities were limited by territorial behavior in a density-dependent fashion (Newton 1979). These raptors have a breeding biology and behavior that follows the general strategy of other tropical forest birds. These adaptations include a lower reproductive output, high adult survivability, and a protracted breeding season in comparison with Temperate zone raptors (Newton 1979, 1986; Delannoy and Cruz 1988). We verified that this species has the ability to renest if nest failure occurs early in the breeding cycle. Bicolored Hawks had a lower predation rate than cavity-nesting Barred and Collared forest-falcons at the same study site (Thorstrom 1993). Our results support the view that tropical environments tend to select for reduced natality as a life history strategy.

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RED-SHOULDERED HAWK NEST SITE SELECTION IN NORTH-CENTRAL MINNESOTA

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ABSTRACT.—We evaluated characteristics at Red-shouldered Hawk (*Buteo lineatus*) nest sites at two study areas with different topography and forest types in north-central and central Minnesota to identify nest site commonalities across geographically distinct areas. During the breeding seasons of 1994–1995, we located nests of Red-shouldered Hawks at the Camp Ripley Army National Guard Training Site and the Chippewa National Forest using a combination of broadcast surveys, helicopter searches, and systematic foot searches. All 38 nests at Camp Ripley and 18 nests in the Chippewa National Forest were in upland hardwood stands; the remaining two nests in the Chippewa National Forest were in aspen (*Populus* spp.) stands. We aged cores from 19 nest trees at Camp Ripley and measured habitat characteristics in a 0.04 ha circle centered on each nest tree and at a paired random site within the nest stand. We compared habitat variables at nest and random sites to identify habitat characteristics that were consistent predictors of nest sites versus random sites for each study area and for all nests combined. Compared to random sites, nest sites in the Chippewa National Forest had larger diameters at breast height (dbh) of the nest tree, taller nest tree height, and higher canopy height. At Camp Ripley, nest sites differed from random sites with regard to many more variables; nests were located in portions of the stand with larger trees and closer to surface water. Nest trees ranged in age from 50–89 years. Logistic regression models indicated that, for both study areas combined, nest tree dbh, basal area, canopy height, and distance to water were the most important variables in distinguishing nest sites from random sites. *Received 31 August 1999, accepted 12 Feb. 2000.*

Red-shouldered Hawk (*Buteo lineatus*) population declines (Brown 1971, Bednarz et al. 1990), projected increases in rates of timber harvest (Jaakko Pöyry Consulting 1992), and observations that canopy thinning may result in displacement of Red-shouldered Hawks by Red-tailed Hawks (*Buteo jamaicensis*; Bryant 1986) have led to increased concern about the availability of nesting habitat for Red-shouldered Hawks in Minnesota and elsewhere. Descriptions of Red-shouldered Hawk nesting habitat have been reported from bottomland forests in eastern, central, and south-central parts of the U.S. (Henny et al. 1973; Bednarz and Dinsmore 1981, 1982; Preston et al. 1989) and from upland mixed forests in the eastern U.S. and southern Canada (Portnoy and Dodge 1979, Armstrong and Euler 1982, Morris et al. 1982, Bosakowski et al. 1992). Red-shouldered Hawk nest sites have been distinguished from generally available forested habitat (as defined by a canopy height ≥10 m) within several km of the nest (Titus and Mosher 1981, Morris and Lemon 1983, Mosher et al. 1986, Preston et al. 1989) or from nest sites of other raptor species (Armstrong and Euler 1982) by the presence of mature hardwood stands, although details of vegetation characteristics varied from site to site.

Red-shouldered Hawk populations in Minnesota have been predicted to decline in the future (Jaakko Pöyry Consulting 1992) based on studies of habitat use from other portions of the species' breeding range and the projected increase in harvest rates of northern hardwood forests. The only previous description of nest site habitat characteristics for Red-shouldered Hawks in Minnesota came from four nests in the southeast corner of Minnesota along tributaries of the Mississippi River and from four nests in north-central Minnesota (Mosher 1987). Within-stand habitat characteristic comparisons in Minnesota may suggest which attributes of nest sites influence

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habitat selection and are associated with successful nesting, and allow managers to better incorporate Red-shouldered Hawk management into forest harvest strategies. We describe Red-shouldered Hawk nest sites in central and north-central Minnesota at the northern edge of the species' breeding range, compare nest sites to random sites within the nest stand, compare habitat characteristics at successful versus unsuccessful nests, and describe logistic regression models that identify habitat characteristics that appear to be associated with nest site selection within the stand.

STUDY AREA AND METHODS

Study area.—We conducted the study at two sites in central and north-central Minnesota: the Camp Ripley Army National Guard Training Site and neighboring state and private land (hereafter Camp Ripley); and the Chippewa National Forest (hereafter the Chippewa). The Camp Ripley Army National Guard Training Site (46° 15′ N, 94° 25′ W) covers approximately 20,000 ha in Morrison County and is bounded by the Crow Wing River on the north and the Mississippi River on the east. Neighboring areas included The Nature Conservancy Lake Alexander Preserve (approximately 1400 ha; 46° 11′ N, 94° 30′ W) and the Pillsbury State Forest (approximately 1300 ha; 46° 22′ N, 94° 26′ W). The northern half of the Camp Ripley Army National Guard Training Site is a glacial moraine characterized by irregular rolling hill topography with interspersed wetlands and vegetated primarily by upland hardwood forest. This area contains two contiguous, approximately 375 ha blocks of mature (50–75 years old) hardwood forest. The Nature Conservancy Lake Alexander Preserve consists of largely contiguous upland hardwood forests with a network of old logging trails and scattered overstory red (*Pinus resinosa*) and white pine (*P. strobus*). Pillsbury State Forest consists of a mosaic of even-aged (50–70 years old) upland hardwood stands with scattered overstory pine, regenerating aspen (*Populus* spp.) stands of varying ages and sizes, pine plantations, and secondary roads and trails.

The Chippewa covers approximately 600,000 ha of Cass and Itasca counties in north-central Minnesota, in the transition zone from hardwood to boreal forest. Northern hardwood stands are scattered through the forest, generally in patches smaller than 30 ha and are interspersed with ash (*Fraxinus* spp.) swamps, marshes, and other wet areas. The most extensive area of hardwoods on the Chippewa, on the north side of Leech Lake (47° 15′ N, 94° 25′ W), covers approximately 6400 ha and contains several stands of at least 100 ha. This area lies on the Guthrie till plain; soils are wet and topography is generally flat. These stands were last logged early in the 20th century. For a more detailed description of the study areas, see McLeod and Andersen (1998).

Locating nests.—We located Red-shouldered Hawk nests using a variety of methods. In 1991 and 1992 at Camp Ripley and in 1994 and 1995 on Camp Ripley and the Chippewa, we used audio broadcasts to survey for Red-shouldered Hawks in a variety of forest types. Preliminary surveys in 1991 and 1992 at Camp Ripley consisted of broadcasting Red-shouldered Hawk alarm calls from roads 3 times for 20 seconds at 3 minute intervals. We broadcast calls at 90 different locations (separated by ≥0.6 km along roads) throughout all forested portions of Camp Ripley, where forest stands were at least 30 years of age. In 1994 and 1995, surveys consisted of broadcasting six sets of Red-shouldered Hawk alarm calls or Great-horned Owl (*Bubo virginianus*) hoots at 1 minute intervals and listening and looking for Red-shouldered Hawk responses (see McLeod and Andersen 1998 for survey protocol details). We detected Red-shouldered Hawks in areas of mature hardwood forest; consequently, we focused searches for nests on this forest type. In 1995, we systematically searched two approximately 375 ha forest blocks at Camp Ripley for nests before the leaves came out with one to four observers scanning for nest structures and walking parallel transects approximately 50 m apart. We also used helicopter searches in portions of Camp Ripley following the methodology of Cook and Anderson (1990). We conducted foot searches at both study areas in 1994 and 1995 as follow-ups to responses from broadcast surveys (McLeod and Andersen 1998) or checks of historic nest sites. In 1995, we searched areas where Red-shouldered Hawks had been detected after tree leaf development in 1994 hindered searching for nests. Local residents or personnel from field crews conducting unrelated research reported six nests in the Chippewa. We determined stick structures to be Red-shouldered Hawk nests either by the presence of an adult Red-shouldered Hawk in or near the nest or by the presence of fresh greenery or down feathers on the nest and vocalizing adult Red-shouldered Hawks in the vicinity. We located one nest in the Chippewa late in the season and determined it to be a Red-shouldered Hawk nest by the presence of molted Red-shouldered Hawk feathers on the ground under the nest. We used binoculars to monitor nests from the ground every 5–10 days. Because young were difficult to detect after they left the nest, we defined a nest as successful if at least one chick survived to 28 days of age [approximately 65% of the average nestling period of 43 days (Crocoll 1994)]. We based nestling age estimates on feather growth (J. Stravers, unpubl. data). Because we could not always determine whether eggs had been laid, we defined unsuccessful nests as those that did not produce young at least 28 days of age, regardless of whether we observed incubation.

For our results to be useful in describing characteristics that distinguish nest sites from available habitat, we needed to locate nests in a manner that did not result in sampling biases (see Daw et al. 1998). We focused our search efforts on mature northern hardwood forest because the literature and preliminary broadcast surveys at both study areas suggested Red-shouldered Hawks would be found in that forest type. However, in 1994 we ran repeated broadcast surveys in the Chippewa in a variety of forest types (including aspen-birch, pine, cedar, and fragmented bottomland hardwoods) and did not hear any vocalizations from Red-shouldered Hawks in forest types other than northern hardwoods (M. A. McLeod, unpubl. data). Although we found some nests as the result of responses to broadcast surveys from roads, birds responded from nests as far as 800 m from survey stations (M. A. McLeod, unpubl. data). We also thoroughly searched approximately 775 ha at Camp Ripley on foot for nest structures without regard to the presence of roads, and additional areas were searched from the air. The responsiveness of Red-shouldered Hawks to broadcast surveys (McLeod and Andersen 1998), coupled with the ubiquitous nature of roads in our study areas, suggests our sample was not biased toward nests located near roads and we are aware of no other potential location bias.

Measurement of site characteristics.—After young fledged or the nest failed, we measured habitat characteristics (Table 1) at all nest sites following a modification of methods outlined by James and Shugart (1970). We defined the nest site as the 11.3 m radius (0.04 ha) circle centered on the nest tree. For each nest site, we located a random point within the nest stand in a random compass direction and at a random distance 75–200 m from the nest tree. We defined the nest stand as an area with the same forest type and comparable stocking density as the nest site and not separated from the nest by roads or harvested areas. We centered each random site on the tree at least 23 cm diameter at breast height (dbh; diameter of the smallest Red-shouldered Hawk nest tree found in 1994) nearest to the random point. Except for variables specific to the nest, we made the same measurements at random sites as at the nest sites.

We cored 25 nest trees at Camp Ripley using an increment borer. Six cores were incomplete because of heart rot and were excluded from analyses. We aged aspen cores using a modification of Campbell (1981; W. H. Lane, pers. comm.) from the cork cambium toward the center, adding five years to adjust for the 1.37 m drilling height (K. Puettmann, pers. comm.).

Data analyses.—We used two-tailed paired t-tests to determine which of the 26 habitat variables (except for slope direction) common to nest and random sites potentially differed ($P < 0.05$) between nest sites and random sites in the Chippewa, at Camp Ripley, and for both areas combined. Subsequent to univariate tests, we constructed logistic regression models (see below) to evaluate the simultaneous influence of habitat variables; thus, we did not attempt to control experiment-wise error by adjusting for multiple comparisons in univariate tests. We used Raleigh tests (Zar 1998) for random angular distribution to evaluate downhill slope direction of nest sites in the Chippewa and at Camp Ripley. We used Bonferroni Z-statistics (as reviewed by Alldredge and Ratti 1992 and using the modification suggested by Agresti and Coull 1998) to determine which tree species were used out of proportion to their availability (simultaneous $\alpha = 0.05$). We used two-tailed t-tests to compare habitat characteristics at successful versus unsuccessful nests at Camp Ripley. We excluded the two nest sites where breeding occurred in both years and young were fledged in one year but not the other from the analysis of factors potentially related to nesting success. We also excluded the five nests where egg laying was confirmed (incubation or chicks observed) and failure occurred more than one week after the median hatch date because nest failures that occur more than one week after hatching are likely to be the result of factors other than those that cause failures earlier in the nesting season (Newton 1979). We calculated failure dates for unsuccessful nests as the day halfway between the last observed activity and the date when no further activity was observed, and we determined hatching dates for individual nests by back-dating from the estimated age of the oldest chick in the nest as determined upon banding ($n = 12$) or from observation of chicks ($n = 16$). Nests in the Chippewa were not included in the analysis of successful versus unsuccessful nests because of the low number of successful nests ($n = 2$).

In addition to univariate comparisons, we used nominal logistic regression (Fienberg 1980) to model the predictive power of habitat variables in determining whether sites were nest or random locations. We used cluster analysis to reduce the number of predictor variables used in the logistic models. For each variable, we calculated the difference between the value at a nest site and the average of the values at the nest and paired random site. We clustered these differences for the combined study areas using average linkage (SAS Institute, Inc. 1994). For each cluster joined within a distance of 1.3, we chose one variable based on its usefulness in describing stand structure or common use by foresters to be included in the modeling. We included a variable that identified the nest site and its paired random site in all models to block for location effects.

We created logistic regression models by forward selection on the habitat variables remaining after cluster analysis. We ordered these variables randomly and entered the first two variables into the model. We eliminated the variable with the lower likelihood ratio χ^2 if its P value was greater than 0.05. We added variables one at a time, in predetermined random order, and after each addition eliminated the variable with the lowest χ^2 value if its P value was greater than 0.05. We terminated variable selection if the addition of a variable resulted in a perfect fit and failure of the model to converge or when all predictor variables had been evaluated in the model selection procedure. For each grouping of nests (Chippewa, Camp Ripley, all) we created ten different random orders of variables and conducted forward selection for each random order. We also created a model to test for interactions between site and habitat variables that appeared consistently ($\geq 50\%$ of models) in the models of all nests.

TABLE 1. Sample means ($\bar{x}$) and standard deviations (SD) for variables measured or derived at all Red-shouldered Hawk nest sites and paired random sites, Chippewa National Forest, Camp Ripley, and both sites combined, 1994 and 1995. Sample size indicates number of nests at each site. An asterisk (*) indicates that nest sites differed from their paired random points (paired *t*-tests, $P < 0.05$).

	Chippewa (n = 20)				Ripley (n = 38)				Both (n = 58)			
	Nest		Random		Nest		Random		Nest		*Random*	
Variable	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	*SD*	$\bar{x}$	SD
Distance from the ground to the bottom of the nest^{a,b} (m)	13.2	1.9	—	—	14.6	2.2	—	—	14.1	2.2	—	—
DBH of the plot-center tree (cm)	47.1*	9.2	37.0	9.0	41.7*	7.7	35.5	8.4	43.6*	8.6	36.0	8.6
Height of the plot-center tree^a (m)	24.2*	2.6	22.1	3.3	25.0*	2.7	22.7	3.2	24.8*	2.7	22.5	3.3
Nest height/plot-center tree height × 100 (%)	54.7	5.7	—	—	58.4	8.1	—	—	57.2	7.5	—	—
Elevation of the plot^c (m)	421.2	11.5	420.0	10.2	403.8*	21.7	408.3	21.0	409.8*	20.5	412.4	18.7
Slope across the plot^d (deg)	2.4	1.9	3.0	2.6	6.3	4.3	6.9	4.9	4.9	4.1	5.6	4.6
Canopy closure at the nest tree^e (%)	93.4	3.8	93.9	3.5	92.1	4.9	92.0	4.5	92.6	4.7	92.7	4.2
Canopy closure in the four quadrants^f (%)	93.8	2.9	93.6	2.6	92.7	3.1	92.2	3.3	93.1	3.1	92.7	3.1
Canopy closure of the plot^g (%)	93.7	3.0	93.7	2.7	92.6	3.2	92.2	3.2	93.0	3.2	92.7	3.1
Canopy height (m); average of 4 readings, one in each quadrant^a	18.6*	2.3	17.2	1.9	19.4*	2.4	17.7	3.0	19.1*	2.3	17.5	2.7
Understory cover^h (%)	66.9	12.5	71.6	10.5	80.1	13.6	81.3	14.5	75.6	14.7	78.9	13.8
Ground cover^h (%)	49.1	11.0	44.2	17.1	56.6	23.9	57.1	25.2	54.3	20.7	52.5	23.2

TABLE 1. CONTINUED.

Variable	Chippewa (n = 20)				Ripley (n = 38)				Both (n = 58)			
	Nest		Random		Nest		Random		Nest		*Random*	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	*SD*	$\bar{x}$	SD
Number of shrubs within 5 m of plot center[i]	100.6	82.5	101.8	78.1	66.0	57.1	77.5	77.7	77.9	68.3	86.3	78.6
Height of dominant shrub species (m)	2.1	0.9	2.2	1.2	1.5*	0.7	1.9	1.3	1.7	0.8	2.0	1.2
Basal area for all trees in the plot[j] (m^2/ha)	34.2	6.9	32.4	8.4	27.6*	7.8	23.2	6.3	29.9*	8.1	26.4	8.3
Average dbh for all trees in the plot[j] (cm)	22.8	2.8	22.4	3.3	22.0*	3.7	20.1	2.8	22.3*	3.4	20.9	3.1
Average dbh for all overstory trees on the plot[k] (cm)	31.4	4.0	30.3	5.9	32.8*	6.1	28.9	4.9	32.3*	5.4	29.4	5.3
Number of overstory trees[k]	14.9	4.5	15.9	7.8	10.8	5.0	11.1	4.4	12.2	5.2	12.8	6.1
Number of understory trees[l]	11.5	4.5	10.8	3.8	12.6	5.4	12.6	5.3	12.2	5.1	12.0	4.9
Number of dead stems $\geq$ 8 cm dbh and $\geq$ 2 m in height	3.3	2.0	3.6	3.6	3.1	2.5	3.9	2.4	3.1	2.3	3.8	2.9
Total number of trees[j]	29.7	7.8	30.2	7.6	26.5	8.8	27.6	7.1	27.6	8.5	28.9	13.1
Distance to surface water[m] (m)	88.8	73.7	86.9	75.5	108.2*	99.6	136.6	119.9	101.5*	91.3	119.5	108.6
Distance to a road (m; 4WD track, gravel, or paved)[m]	328.9	254.8	323.9	252.6	282.3	169.1	284.0	192.4	298.3	201.8	297.8	213.7

TABLE 1. CONTINUED.

Variable	Chippewa (n = 20)				Ripley (n = 38)				Both (n = 58)			
	Nest		Random		Nest		Random		Nest		*Random*	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	*SD*	$\bar{x}$	SD
Distance to nearest harvest activity^m (m)	286.5	186.4	276.2	155.5	327.0	219.7	338.0	193.8	313.0	208.1	316.7	182.5
Trees in the plot 8–12.4 cm dbh (%)	24.3	11.1	26.4	10.1	27.5	12.9	31.5	14.2	26.4	12.3	29.7	13.1
Trees in the plot 12.5–22.6 cm dbh (%)	31.6	9.9	32.5	13.7	33.0	13.4	32.0	14.0	32.5	12.2	32.1	13.8
Trees in the plot 22.7–37.8 cm dbh (%)	29.4	9.1	27.7	10.9	26.8	14.2	29.5	14.2	27.6	12.7	28.9	13.1
Trees in the plot ≥37.9 cm dbh (%)	14.7	9.1	13.4	9.6	12.8*	10.9	7.0	6.9	13.4*	10.0	9.2	8.4

[a] Height was measured using a clinometer. Distances used to calculate height were measured with a tape.

[b] Variable is specific to the nest tree and therefore not applicable to random sites.

[c] Determined from 7.5 min U.S. Geological Survey (USGS) quadrangle maps.

[d] Measured with a clinometer.

[e] Measured using a convex densiometer. Four readings were taken, one in each cardinal direction, facing away from the nest tree. If necessary, the observer stepped away from the nest tree so the bole was not counted as a significant portion of the canopy.

[f] Measured with a convex densiometer at 8.5 m from plot center in each of the four cardinal directions. Four readings were taken at each point, one in each cardinal direction. All 16 measurements were averaged.

[g] Average of the 16 quadrant canopy closure and four nest tree canopy closure measurements.

[h] Measured at 1-m intervals between 1 and 10 m, inclusive, from plot center in each cardinal direction, using an ocular tube as described in James and Shugart (1970).

[i] A shrub was any live woody stem <8 cm dbh and >50 cm in height. Stem numbers were counted at a height of 10 cm.

[j] A tree was any live stem >8 cm dbh.

[k] An overstory tree was any live stem >8 cm dbh whose major foliage fell in the upper third of the overall stand height.

[l] An understory tree was any live stem >8 cm dbh whose major foliage fell in the bottom two thirds of the stand height.

[m] Distance was paced if <100 m; otherwise it was estimated from 1:15,400 aerial photographs or 7.5 min USGS quadrangle maps.

We eliminated cross terms with $P > 0.05$ one at a time, starting with the highest P value, until all remaining terms had $P < 0.05$. We used logistic regression rather than discriminant function analysis because logistic regression does not depend on normality of the data (Fienberg 1980). All statistical analyses used JMP® software (version 3.1.5 for Macintosh, SAS Institute, Inc. 1994).

RESULTS

We located 5 Red-shouldered Hawk nests in the Chippewa in 1994 and 15 additional nests in 1995. None of the 1994 nests was reused in 1995, nor did we find active nests in 1995 in the vicinity of any of the 1994 nests. Of the 20 nests, 17 were unsuccessful and 2 produced a single chick each. Success of the remaining Red-shouldered Hawk nest was undetermined because we located it late in the season, after all nestlings in our sample of nests had fledged. Abundant whitewash beneath the nest suggested that at least one chick reached fledging age. Eighteen of the 20 nests were in mature northern hardwood stands; the remaining two were in mature aspen stands. Nests were found in paper birch (*Betula papyrifera*; 5), sugar maple (*Acer rubrum*; 5), yellow birch (*B. alleghaniensis*; 3), quaking aspen (*Populus tremuloides*; 3), red oak (*Quercus rubra*; 2), bur oak (*Q. macrocarpa*; 1), and balsam poplar (*P. balsamifera*; 1). Nest tree use did not differ from availability for any tree species.

We located 19 nests at Camp Ripley in 1994. In 1995, 10 of these nest structures appeared to be used by Red-shouldered Hawks, and we located 19 additional nests, none of which was in breeding areas where we had found nests in 1994. Thirteen of the 19 nests produced young in 1994. In 1995, 15 of the 29 nests produced young. We found nests in quaking aspen (20), red oak (12), big-tooth aspen (*Populus grandidentata*; 3), paper birch (2), and white oak (*Quercus alba*; 1). All nests were in mature upland hardwood stands. Nest trees were not selected in proportion to their availability ($z = 5.49$, $P < 0.001$), with quaking aspen used more than expected. Nests at both study sites tended to be in large diameter trees in closed canopy mature forest and close to water (Table 1). Nest tree age at Camp Ripley averaged 59 years (range: 50–76, $n = 8$) for aspen and 67 years (range: 54–89, $n = 11$) for oak.

Nest sites in the Chippewa had larger nest tree dbh and higher nest tree height and canopy height than their paired random sites ($t = 4.21$, $P < 0.001$; $t = 2.38$, $P = 0.03$; $t = 2.13$, $P = 0.047$; respectively: 19 df for all tests) as did nest sites at Camp Ripley ($t = 3.33$, $P = 0.002$; $t = 2.98$, $P = 0.005$; $t = 2.76$, $P = 0.009$; respectively: 37 df). Relative to their paired random sites, nest sites at Camp Ripley were also at a lower elevation and closer to permanent water ($t = -3.41$, $P = 0.002$; $t = -3.06$, $P = 0.004$; respectively: 37 df), and had shorter shrub height, larger basal area, larger average dbh of all trees, larger average dbh of overstory trees, and a higher percentage of large (≥37.9 cm dbh) trees ($t = -2.09$, $P = 0.04$; $t = 2.88$, $P = 0.007$; $t = 2.89$, $P = 0.006$; $t = 3.29$, $P = 0.002$; $t = 2.93$, $P = 0.006$; respectively; 37 df). Downhill slope direction of nest sites at Chippewa was not significantly different from random (Rayleigh's $z = 2.090$, $n = 17$, $R = 5.96$, $P > 0.05$) but at Camp Ripley nest sites were located more often on north-facing sites (mean direction = 32°, Rayleigh's $z = 4.244$, $n = 38$, $R = 12.70$, $P = 0.01$). At Camp Ripley, successful nests had more small trees (8–12.4 cm dbh; $t = 2.30$, 29 df, $P = 0.03$) and were closer to harvest activity ($t = 3.14$, 29 df, $P = 0.004$) than random sites.

Cluster analysis reduced the number of potential predictor variables in the logistic regression modeling from 26 to 19. Canopy cover of the plot was selected from a cluster with canopy cover at the nest tree, canopy cover away from the nest tree, ground cover, understory cover, number of snags, and shrub height. Diameter at breast height of overstory trees was chosen from a cluster with average dbh of all trees in the plot. Of the 19 remaining habitat characteristics, nest tree dbh and percent of medium-small (12.5–22.6 cm dbh) trees were statistically significant predictors of nest sites versus random sites in the Chippewa in more than 5 logistic regression models. Distance to permanent water, percent of small (8–12.4 cm dbh) trees, percent of large (≥37.9 cm dbh) trees, canopy height, number of understory trees, total number of trees, and distance to a road were significant in 1–4 of the 10 models. Five of the models terminated in perfect fits. At Camp Ripley, distance to permanent water, nest tree dbh, basal area, distance to a road, and average dbh of overstory trees were statistically significant predictors in at least 5 models, and 10 variables were significant in 1–4 models. When all nest sites were analyzed together, nest tree dbh, distance to permanent water, basal area, and canopy height were significant in 5 or more models. Average dbh of overstory trees, number of overstory trees, distance to harvest activity, elevation, slope, percent of small trees, and percent of medium-small trees were significant in 1–4 models. Basal area and distance to permanent water interacted significantly with study area, but nest tree dbh and canopy height did not. For both basal area and distance to permanent water, parameter estimates indicated the variables were important predictors at Camp Ripley but not in the Chippewa.

DISCUSSION

The significance of nest tree dbh and nest tree height in univariate tests for both study areas and the consistent appearance of nest tree dbh as a significant predictor of nest site in logistic regression models indicate that within mature hardwood stands in central and north-central Minnesota, Red-shouldered Hawks selected relatively large trees in which to place their nests. These results are consistent with other studies (Bednarz and Dinsmore 1982, Woodrey 1986, Titus and Mosher 1987, Johnson 1989). The selection of quaking aspen out of proportion to its availability is probably the result of differences in growth forms. Aspens and birches often form crotches capable of supporting nests, whereas other canopy and overstory trees, such as American basswoods (*Tilia americana*), seldom do. Other authors (Bednarz and Dinsmore 1982, Morris et al. 1982, Titus and Mosher 1987) have suggested that tree structure rather than species is important in nest tree selection.

Nest sites also differed from random sites. Canopy height was higher at nest sites than at random sites at both study areas, indicating that the trees surrounding the nest, as well as the nest tree, were taller than trees at the corresponding random sites. Preston and coworkers (1989) reported that Red-shouldered Hawk nest sites in Arkansas had a taller canopy than sites selected randomly in the same forest type, and Woodrey (1986) found that nest sites in Ohio had taller canopies than random plots located within 75 m of the nest.

There was a tendency at Camp Ripley for Red-shouldered Hawks to avoid placing their nests on south-facing slopes. Johnson (1989) also reported this trend for Red-shouldered Hawk nests in north-central New York. It is unclear why Red-shouldered Hawks would prefer one aspect to another. In the Chippewa, slope is so slight that aspect is unlikely to have any effect on exposure of the nest. Slopes are steeper at Camp Ripley and their direction might be more likely to affect microclimate at the nest.

Several variables that did not differ between nest and random sites in the Chippewa differed at Camp Ripley. Elevation and distance to permanent water differed between nest and random sites at Camp Ripley, and distance to permanent water was significant in every Camp Ripley logistic regression model, suggesting Red-shouldered Hawks at Camp Ripley place their nests close to water. The upland hardwood areas of Camp Ripley have irregular rolling hills that typically rise 10–35 m above adjacent wetlands and ponds, so a site near water also tends to be lower in elevation than the surrounding area. Other researchers have found Red-shouldered Hawks to be associated with riparian areas and wetlands (Henny et al. 1973, Portnoy and Dodge 1979, Bosakowski et al. 1992). In the Chippewa, 14 of the 20 nests were in the flat Guthrie till plain. Ash swamps, marshes, and bogs are interspersed throughout the area. Both nest and random sites in the Chippewa tended to be closer to water than nest sites at Camp Ripley, suggesting that the ubiquitous nature of water in this part of the Chippewa removes proximity to water as a factor in Red-shouldered Hawk nest site selection. These results do not indicate that habitat characteristics that were factors in nest site selection in one area do not influence nest site selection in another. Rather, the predominance of some habitat features, such as water, in some landscapes makes it difficult to detect the importance of these features because all potential sites are acceptable with regard to that character.

Forest characteristics indicating the presence of large trees were significant in distinguishing nest sites from random sites at Camp Ripley but not in the Chippewa. Basal area, average dbh of overstory trees, average dbh of all trees, and percent of large ($\geq$37.9 cm dbh) trees were greater at nest sites than random sites at Camp Ripley. These variables (except average dbh of all trees, which was eliminated from modeling during cluster analysis) also were significant in at least one logistic regression model, with basal area and average overstory dbh being significant in 5 of the 10 models. Morris and Lemon (1983) and Titus and Mosher (1981) also reported larger basal area at nest sites than at random sites, and Woodrey (1986) reported a greater number of trees larger than 50 cm dbh at nest sites than at random sites. The significance of these variables at Camp Ripley but not in the Chippewa may be the result of overall larger basal area in the Chippewa. Basal area was larger at random sites in the Chippewa than at nest sites at Camp Ripley (t-test: $t = 2.17$, 56 df, $P = 0.03$). Similarly, average dbh of all trees and percent of large ($\geq$37.9 cm dbh) trees were larger at Chippewa random sites than at Camp Ripley random sites ($t = 2.79$, 56 df, $P = 0.007$; $t = 2.93$, 56 df, $P = 0.005$; respectively), while values at nest sites were comparable between the two study areas (Table 1). These results indicate that sites with large trees were more abundant in the Chippewa than at Camp Ripley.

When all data were combined for logistic regression modeling, nest tree dbh, distance to permanent water, basal area, and canopy height were consistently significant predictors of nest sites versus random sites. The model using cross terms was created to investigate the possibility that a variable might be significant at one area but not the other. Basal area and distance to permanent water were significant at Camp Ripley but not in the Chippewa. These results are consistent with the univariate analyses that indicate both large trees and water were more abundant in the Chippewa than at Camp Ripley. These variables appeared in the models of all nests because sample size at Camp Ripley was twice that of the Chippewa. Thus, nest tree dbh and canopy height were the only two variables that were consistent predictors of nest sites versus random sites across study areas, indicating selection of sites with large trees. These results suggest that young forests are less suitable as nest sites for Red-shouldered Hawks than mature stands with large trees. Cutting rotations of less than 50 years would not allow trees to reach the minimum age of the nest trees used in this study.

Several variables that did not differ between nest and random sites in paired t-tests and were not useful by themselves in separating nest sites from random points in logistic regression models were significant predictors of nest versus random sites in logistic regression models when paired with other variables. For example, percent of medium–small trees by itself was not useful in separating nest sites from random sites in the Chippewa, but the model with percent of medium–small trees and nest tree dbh was a better predictor of nest sites versus random sites than either variable alone. Although there may be an interaction between the variables that makes their combination a better predictor, it seems more likely that spurious relationships between variables with small samples sizes result in apparent significance when there is none. Only 3 of the 20 nest trees in the Chippewa were smaller than their paired random trees; if the site with the largest negative difference between size of the nest tree and the paired site center tree is eliminated from the analysis, percent of medium–small trees is no longer a significant predictor of random versus nest sites. That the removal of one nest from the data set changes the models so dramatically suggests that percent of medium–small trees, and probably other variables that were not significant in paired t-tests, do not have any biological significance in discriminating nest sites from random sites. The frequent occurrence of perfect fit models when data from the two study areas were analyzed separately also was probably attributable to small sample sizes.

Red-shouldered Hawks appeared to select sites close to water and with large trees when choosing nest locations, but there was no evidence that these habitat characteristics affected nesting success at Camp Ripley. The two habitat features that differed between successful and unsuccessful nests indicate more small trees and a closer distance to harvested areas at successful nests. These features may relate to habitat quality (perhaps prey availability), or may simply be a statistical artifact. Other researchers (Bednarz and Dinsmore 1981, Armstrong and Euler 1982) have suggested Red-shouldered Hawks need large forest blocks for successful breeding and avoid openings and human activities. Forest edge is also important to Red-shouldered Hawks as foraging habitat (Craighead and Craighead 1956, Bednarz and Dinsmore 1981), although in these cases openings were provided by wetlands and not harvested upland area.

Despite apparently higher availability of suitable nest sites in the Chippewa than at Camp Ripley, productivity in the Chippewa was lower than at Camp Ripley. Sixty percent of nests at Camp Ripley fledged young, whereas at most 15% of the nests found in the Chippewa fledged young. The fledging rate in the Chippewa was also lower than reported in other studies (Henny et al. 1973, Wiley 1975, Crocoll and Parker 1989). Factors unrelated to nest site availability might be responsible for low nesting success in the Chippewa. Light weights of chicks and chicks dying in the nest (M. A. McLeod, unpubl. data) were consistent with low food availability. With only two years of data it is impossible to determine whether low reproductive rates in the Chippewa were the result of annual variation or are chronic. If nesting success at the northern edge of the breeding range is consistently low regardless of forest structure, these populations may be maintained through immigration from other, more productive areas.

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AGE AND SEX DIFFERENCES IN THE TIMING OF FALL MIGRATION OF HAWKS AND FALCONS

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ABSTRACT.—We trapped more than 23,000 migrating raptors at Cedar Grove, Wisconsin during the autumns of 1953–1996, permitting accurate identification of age and sex. Adults migrated significantly later than juveniles in 8 of 10 species, and males migrated later than females in 7 species. We suggest that it is adaptive for adults and males to remain on breeding territories as long as possible. Adult Peregrine Falcons (*Falco peregrinus*) migrated before juveniles. There was no age difference in migration of Rough-legged Hawks (*Buteo lagopus*). Both species breed in the Arctic where the brief breeding season requires that adults leave as soon as possible so adults might then migrate more rapidly than juveniles. We compare our results with those of 16 other studies. Juveniles migrated significantly later than adults in 8 of 13 species at Falsterbo in southern Sweden (Kjellén 1992). Falsterbo is more than 12° latitude (1300 km) north of Cedar Grove and the breeding range of most of the species occurring there extends north of the Arctic Circle, where birds suffer from the same abbreviated breeding seasons as do the Peregrine Falcon and Rough-legged Hawk in North America. Adult females migrated after adult males in the two large species of *Accipiter*; this may be because the females, not the males, establish and maintain territory in these species. *Received 16 April 1999, accepted 13 Feb. 2000.*

It has been known for more than 60 years that there are age and sex differences in winter distribution and the timing of migration of birds (Eaton 1933, Nice 1937). Relatively few studies have provided data on the differences occurring during fall migration. Kerlinger (1989) listed 7 hypotheses that have been proposed to explain age or sex differences in the timing of migration or the wintering areas of birds: (1) The migration threshold hypothesis (Baker 1978) is an all inclusive, complex multifactorial approach, probably including all of the other hypotheses. This hypothesis is untestable (Ketterson and Nolan 1983), hence it cannot be falsified and it makes no predictions. (2) The character divergence hypothesis (Koplin 1973) explains habitat segregation in wintering birds as a mechanism to avoid competition between the sexes. But this merely substitutes intrasexual competition for intersexual and is possible only if one invokes group selection (Jehl 1970, Mueller 1990); it also makes no predictions. (3) The arrival time hypothesis (King et al. 1965, Myers 1981) predicts that the sex engaged in intrasexual competition for access to mates would migrate earlier in spring and winter closer to the breeding area, but it makes no predictions for fall migration. (4) The physiological hypothesis (Ketterson and Nolan 1976) states that large birds are better able to withstand the rigors of northern winters and thus winter farther north, and by extension, migrate later in fall. Female raptors are larger than males and thus would be expected to migrate later in fall. (5) The social dominance hypothesis (Mueller et al. 1977, Gauthreaux 1978) holds that the larger sex forces the smaller sex to migrate farther and earlier in autumn. Males are the smaller sex in raptors. (6) The molt hypothesis (Smallwood 1988) holds that males migrate after females in autumn because males molt remiges later than females, but only adults molt and this fails to explain sex differences in juveniles. (7) The feeding efficiency hypothesis (Rosenfield and Evans 1980) maintains that juveniles migrate earlier than adults because they are less efficient predators and migrate earlier along with most of their avian prey. Females also migrate before males because the larger prey they hunt more efficiently is scarcer than the smaller prey that is optimal for males, and as the season progresses and more prey birds migrate south, larger prey become even more scarce. We add an eighth hypothesis: young birds migrate earlier than

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adults because of their inexperience in finding a wintering home.

Capturing a hawk during migration permits accurate determination of age and sex. In this paper, we examine data gathered in routine hawk trapping during fall migration in southeastern Wisconsin, compare our results with other studies, and evaluate the various hypotheses.

METHODS

We trapped 23,745 diurnal raptors of 17 species in the autumns of 1953–1996 at the Cedar Grove Ornithological Station (43° 33′ N, 87° 21′ W) on the western shore of Lake Michigan in Sheboygan County, Wisconsin. Sufficient individuals were obtained to distinguish age and sex differences in timing of migration in 8 species and on sex differences in juveniles in 2 additional species.

Sex was determined by plumage in the American Kestrel (*Falco sparverius*), adult male Northern Harriers (*Circus cyaneus*), and adult male Merlins (*Falco columbarius*). Measurements were used to determine sex in juvenile Northern Harriers (Bildstein and Hamerstrom 1980), Northern Goshawks (*Accipiter gentilis*; Mueller et al. 1976), Cooper's Hawks (*A. cooperii*; Mueller et al. 1981), Sharp-shinned Hawks (*A. striatus*; Mueller et al. 1979), Merlins (*Falco columbarius*; Clark 1985a), and Peregrine Falcons (*F. peregrinus*; Ratcliffe 1980). Sex was not determined in Red-tailed Hawks (*Buteo jamaicensis*), Red-shouldered Hawks (*B. lineatus*), and Rough-legged Hawks (*B. lagopus*), but an estimate of sex was obtained by dividing the distribution of hawks trapped into large and small halves based on measurement of wing chord. Age was determined by plumage. Birds with juvenile plumage were classified as HY (hatching year). Many hawks and falcons have not completed their molt during fall migration and the presence of two generations of feathers permits the separation of some adults into SY (second year) and ASY (after second year). Where sample sizes of SY and ASY birds were small we grouped them into AHY (after hatching year) as we did with the adults of species where SY or ASY could not be determined. We began to record molt and the exact plumage of adults consistently in 1962.

The extent of the breeding range to the north of Cedar Grove, and the northernmost and southernmost extent of the wintering range were obtained from Palmer (1988). The same information for Swedish raptors was obtained from Beaman and Madge (1998). The maximum distance of migration is the difference from the northernmost extent of breeding to the southernmost extent of wintering range.

The Mann-Whitney *U*-test was used to compare the timing of migration of age and sex groups. Sample sizes are given in Fig. 1. Comparisons of the proportion of birds trapped early and late in the season were performed with a 2×2 χ^2 test, utilizing Yate's correction. The Fisher exact test was used in one case where sample sizes were too small for χ^2 analysis. Statistics were performed in SYSTAT (Wilkinson 1989) on a MacIntosh computer.

We used several different kinds of traps and lures to capture the raptors, and sex ratios of many species attracted to the traps vary with trap and lure type. The types of traps and lures used varied over the 44 years of the study and a simple analysis of the bias of sex ratios is impossible. Consequently, the data should not be used to estimate sex ratios in nature.

RESULTS

Northern Harrier.—HY birds migrated before AHY (Fig. 1, Table 1). AHY males tended to migrate after AHY females ($P = 0.08$), there was no sex difference in the timing of HY birds. Only 12% of the AHY were identified as SY or ASY; the small samples precluded an examination of differences between the two. More than 7% of the Northern Harriers observed on or before 12 October were trapped, but only 4% of those observed after this date were captured, indicating that AHY are more difficult to trap than HY ($\chi^2 = 28$, 0.001).

Northern Goshawk.—HY hawks migrated before SY and ASY (Fig. 1, Table 1), but there was no difference in timing between SY and ASY in either sex. The only difference between the sexes was between ASY females and males; females migrated later than males. The median date for both males and females was 5 November. We trapped 31 males and 25 females on this date. Essentially half (112 of 225) of the males were captured on or before 4 November; only 42% of the females (86 of 204) were captured on or before 4 November. Only 36% of the males were caught on or after 6 November; over 45% of the females were trapped during this interval. The percentage trapped (57%) remained approximately constant throughout the season, suggesting that AHY were trapped as readily as HY.

Cooper's Hawk.—SY birds migrated later than HY (Fig. 1, Table 1) and ASY migrated later than SY ($P < 0.01$, both sexes). HY males migrated later than HY females, but both SY and ASY females migrated later than males. AHY birds appear to be trapped as readily as HY.

Sharp-shinned Hawk.—SY hawks migrated later than HY (Fig. 1, Table 1), and ASY later than SY. Males migrated later than females.

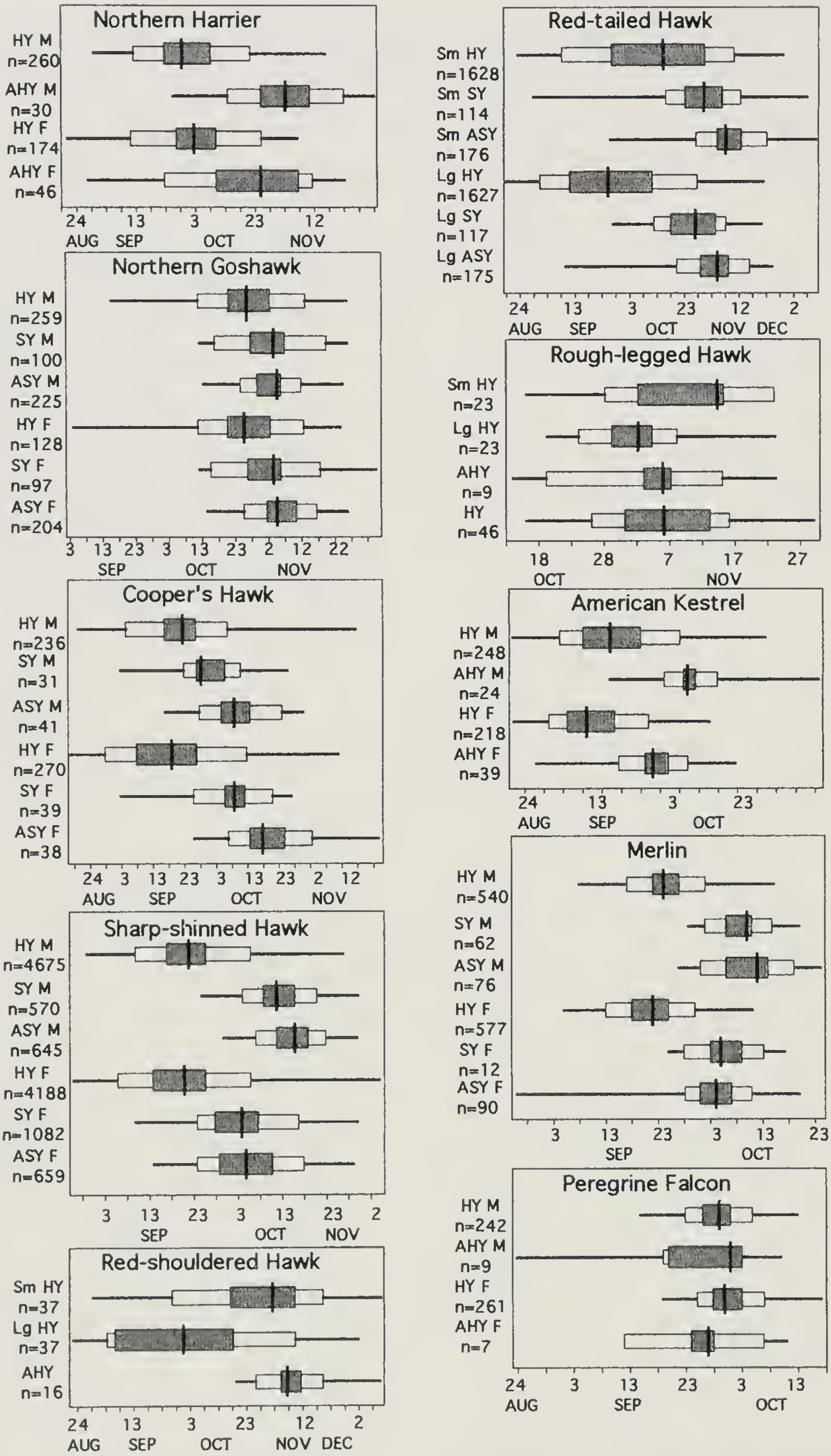

FIG. 1. Temporal distribution of hawks and falcons in autumn migration. HYM: Hatching year males (males in the juvenal plumage). SYM: Second year males (males in first basic plumage with some juvenal feathers. ASYM: After second year males (males with feathers from two basic plumages). AHYM: After hatching year males (males two or more years old). F: females. Sm: Birds with wing chords shorter than the mean. Lg: Birds with wing chords longer than the mean. The vertical line indicates the median date, the shaded bar, ± 16.7% of the birds trapped, the white bar, an additional ± 16.7%, and the horizontal line, an additional ± 14.5%. The three categories thus include 33%, 67% and 95%, respectively.

TABLE 1. Results of Mann-Whitney *U* tests on age and sex differences in timing of migration.

Species	Comparison	Sample sizes	*U*	*P*
Northern Harrier	HY vs AHY males	259, 31	11,245	<0.001
	HY vs AHY females	172, 46	2136	<0.001
	AHY males vs females	31, 46	884	0.08
	HY males vs females	259, 172	21,618	>0.05
Northern Goshawk	HY vs SY males	259, 100	9963	<0.001
	SY vs ASY males	100, 225	11,587	>0.05
	HY vs SY females	128, 97	4915	<0.01
	SY vs ASY females	97, 204	8761	>0.05
	HY males vs females	259, 158	16,722	>0.05
	SY males vs females	100, 97	4980	>0.05
	ASY males vs females	225, 204	19,478	<0.01
Cooper's Hawk	HY vs SY males	236, 31	2532	<0.01
	SY vs ASY males	31, 41	374	<0.01
	HY vs SY females	270, 39	2715	<0.001
	SY vs ASY females	39, 38	383	<0.001
	HY males vs females	236, 270	34,807	0.05
	SY males vs females	31, 39	428	<0.05
	ASY males vs females	41, 38	457	<0.01
Sharp-shinned Hawk	HY vs SY males	4675, 570	151,839	<0.001
	SY vs ASY males	570, 645	141,195	<0.001
	HY vs SY females	4188, 1082	272,150	<0.001
	SY vs ASY females	1082, 659	332,866	<0.05
	HY males vs females	4675, 4188	823,588	<0.001
	SY males vs females	570, 1082	450,556	<0.001
	ASY males vs females	645, 659	328,525	<0.001
Red-tailed Hawk	Sm HY vs Sm SY	1628, 114	123,532	<0.001
	Sm SY vs Sm ASY	114, 176	6913	<0.001
	Lg HY vs Lg SY	1627, 117	14,579	<0.001
	Lg SY vs Lg ASY	117, 175	6954	<0.001
	Sm vs Lg HY	1628, 1627	1,681,435	<0.001
	Sm vs Lg SY	114, 117	7586	<0.05
	Sm vs Lg ASY	176, 175	18,574	<0.001
Red-shouldered Hawk	Sm vs Lg HY	37, 37	929	<0.01
	HY vs AHY	74, 16	339	<0.01
Rough-legged Hawk	Sm vs Lg HY	23, 23	367	<0.05
	HY vs AHY	46, 9	206	>0.05
American Kestrel	HY vs AHY males	248, 24	829	<0.001
	HY vs AHY females	218, 39	1652	<0.001
	AHY males vs females	24, 39	748	<0.001
	HY males vs females	248, 218	32,902	<0.001
Merlin	HY vs SY males	540, 62	3001	<0.001
	SY vs ASY males	62, 76	2732	>0.05
	HY vs SY females	577, 12	627	<0.001
	SY vs ASY females	12, 90	652	>0.05
	HY males vs females	540, 577	128,407	<0.001
	SY males vs females	62, 12	444	>0.05
	ASY males vs females	76, 90	4950	<0.001
Peregrine Falcon	HY vs AHY males	242, 9	1073	>0.05
	HY vs AHY females	261, 7	1126	>0.05
	AHY males vs females	9, 7	33	>0.05
	HY males vs females	242, 261	26,024	<0.001

Almost 22% of the Sharp-shinned Hawks observed on or before 30 September were trapped, but only 14% of those seen after this date were captured, indicating that AHY are more difficult to trap than HY (χ^2 = 684, P < 0.001).

Red-tailed Hawk.—SY hawks migrated later than HY (Fig. 1, Table 1) and ASY later than SY. Small birds migrated later than large birds. Almost 26% of the Red-tailed Hawks observed on or before 4 October were trapped, but only 12% of those seen after this date were captured, indicating that AHY are much more difficult to capture than HY (χ^2 = 463, P < 0.001).

Red-shouldered Hawk.—AHY hawks migrated later than HY (Fig. 1, Table 1). We were able to assign only 3 adults to SY or ASY. Small HY hawks migrated later than large HY; the sample of AHY was too small for analysis. More than 12% of the Red-shouldered Hawks observed on or before 19 October were trapped, but only 4% of those seen after this date were captured, indicating that AHY are much more difficult to trap than HY (χ^2 = 22, P < 0.001).

Rough-legged Hawk.—Although only 9 AHY were captured, the lack of even a hint of a difference (Fig. 1, Table 1) in timing of migration between adults and juveniles suggests that there is no difference. Small juveniles migrated later than large juveniles.

American Kestrel.—AHY kestrels migrated later than HY (Fig. 1, Table 1), and males migrated later than females. We trapped almost 13% of the American Kestrels observed before 22 September, but only 7% of those observed after this date, indicating that AHY are more difficult to capture than HY (χ^2 = 37, P < 0.001).

Merlin.—SY adults migrated later than HY (Fig. 1, Table 1), but there was no significant difference in timing between ASY and SY. HY males migrated later than HY females and ASY males migrated later than ASY females, but there was no significant difference between the sexes in SY, although the sample is small for females. We trapped almost 16% of the Merlins observed before 29 September and less than 4% of those seen after this date, indicating that adults are much more difficult to capture than juveniles (χ^2 = 257, P < 0.001).

Peregrine Falcon.—We found no age differences in the timing of migration in either males or females (Fig. 1, Table 1), but sample sizes for AHY are small. In 1991 through 1995 we made a special effort to identify the age of all Peregrine Falcons seen at Cedar Grove. Of the birds observed before 20 September, 24 were HY, 41 were AHY, and we were unable to determine the age of 21. Of the birds seen after 19 September, 112 were HY, 37 were AHY, and age was not determined for 85. Of the birds for which age was determined, AHY birds clearly migrated earlier than HY birds (χ^2 = 27, P < 0.001). HY females migrated later than HY males (Fig. 1, Table 1). No sex difference was evident in the small sample of AHY birds. We trapped 15% of the Peregrine Falcons observed before 19 September, and 36% of those seen after this date, indicating that adults are much more difficult to capture than juveniles (χ^2 = 11.9, P < 0.001).

DISCUSSION

Age differences in the timing of migration.—In fall adults (AHY) migrated later than juveniles (HY) in 8 of 10 species at Cedar Grove. Three of the eight hypotheses predict this; the social dominance hypothesis also predicts that males migrate before females, but males migrated before females in only 4 of the 22 comparisons of sexes possible in this study. The feeding efficiency hypothesis holds that juveniles migrate earlier than adults because they must migrate along with their avian prey. Of the 10 species in this study only the Sharp-Shinned Hawk and Peregrine Falcon have more than 75% birds in their diet (Snyder and Wiley 1976), and contrary to the prediction, adult Peregrine Falcons migrated before juveniles. Four of the 10 species take less than 10% birds and in 3 of these (Red-tailed Hawk, Red-shouldered Hawk, and American Kestrel) juveniles migrated before the adults. There seems to be no correlation between the prey type and early migration of juveniles. The inexperience with winter home hypothesis makes no prediction other than that juveniles migrate earlier than adults. Another possible explanation for the later migration of adults is that there is some advantage to remaining on the breeding territory as long as possible in the fall. This might facilitate early occupancy and a better ability to defend the territory the following spring. The last two hypotheses appear to offer the best explanation as to why juveniles migrate earlier than adults in most species.

Most of the Peregrine Falcons captured at Cedar Grove are *F. p. tundrius*, which breed in the Arctic and winter to 40° S in Chile and Argentina (White 1968). The species is clearly the longest distance migratory raptor in North America. Newton (1979) noted that adult long distance migrants sometimes depart first in the autumn, travel faster, and reach the wintering areas before the juveniles. He speculated that adults might depart earlier because they are able to reach the body condition needed for migration sooner than recently fledged juveniles and might migrate faster because they know the way. Arctic breeding Peregrine Falcons have barely enough time to complete the breeding cycle before most of their prey have departed for the south (Cade 1960). As the young approach the age of independence, parent-offspring conflict (Trivers 1974) exists, and the attempts of the offspring to maximize their fitness come into conflict with that of their parents. The young selfishly demand more care than the parents should provide. As prey become scarcer, there is an increasing incentive for parents to refuse care, and we propose that the easiest way for them to do this is to leave the breeding territory before their offspring, avoiding the offsprings' incessant and aggressive begging. Alternatively, adults and juveniles may leave the breeding territory simultaneously, but adults migrate more rapidly than juveniles. Peregrine Falcons linger at Assateague Island on the Virginia and Maryland coast where the ratio of juveniles to adults is 5.7:1 (Ward et al. 1988), and at Padre Island, Texas, where the ratio is 3.9:1 (Hunt et al. 1975). The ratio at Cedar Grove, where the birds only fly past, is 1.7:1, closer to what might be expected based on the average number of young fledged and the fact that most Peregrine Falcons do not breed until they are two years old (Palmer 1988). These observations suggest that juveniles are more likely to interrupt migration in habitat suitable for hunting and thus migrate more slowly than adults.

Our results on comparisons of age agree with other studies in 18 of 24 comparisons (Table 2). In 3 of the 6 cases that differ, the results differ significantly in one sample but not in the other. The three remaining studies indicate that juveniles migrated later than adults and our results show the opposite. The account of Kessel and Springer (1966) on Red-tailed Hawks in central Alaska is anecdotal with no data, and cannot be evaluated further. Kjellén (1992) showed that juvenile Northern Harriers and Merlins migrated significantly later than adults at Falsterbo Peninsula in southern Sweden. The data on the Merlin are questionable. Kjellén (1992) found that adult females migrated first, then juveniles of both sexes, and last adult males, with adult males and females combined migrating earlier than juveniles. Adult females are difficult to distinguish from juveniles in the hand, and we find it very hard to believe that Kjellén (1992) was able to identify similar numbers of adult females and adult males in the field. If he was incorrect in his identification of adult females, then it is possible, if not likely, that adults migrated later than juveniles. His observation that juvenile Northern Harriers migrate after adults is more difficult to dispute. Juveniles can be distinguished from adult females if a good view of the bird is obtained, and adult males are easily identified. Kjellén (1992) also presents data on age differences in the timing of migration for nine species of European raptors. The following juveniles migrated significantly earlier than adults: Red Kite (*Milvus milvus*), Marsh Harrier (*Circus aeruginosus*), and the Eurasian Sparrowhawk (*Accipiter nisus*). Adults migrated significantly earlier than juveniles among the following: Honey Buzzard (*Pernis apivorus*), Common Buzzard (*Buteo buteo*), Osprey (*Pandion haliaetus*), and Eurasian Hobby (*Falco subbuteo*). No significant age difference in the timing of migration was noted in Montagu's Harrier (*C. pygargus*) or Eurasian Kestrel (*F. tinnunculus*). Including species that also occur in North America, Kjellén (1992) found that juveniles migrated significantly later than adults in 8 species of raptors and that the opposite was true in 3 species. This ratio of 8 to 3 is a great contrast to the 1 to 8 we observed at Cedar Grove (Fisher exact test, $P = 0.01$).

Kjellén (1992) proposed that adults migrate before juveniles in long distance migrants. In

TABLE 2. Comparisons of Cedar Grove, WI, vs other studies.

Species	Citation	Locality	Finding	This study
Northern Harrier	Bildstein et al. 1984	Duluth, MN	AHY ~ HY[a]	AHY > HY[b]
		Hawk Cliff, ON	AHY > HY	Agrees
		Hawk Mt., PA	AHY > HY	Agrees
		Cape May, NJ	AHY > HY	Agrees
		Cape May, NJ	HYF > HYM	HYF ~ HYM
		Hawk Cliff, ON	HYF ~ HYM	Agrees
		Duluth, MN	HYF ~ HYM	Agrees
		Hawk Mt., PA	HYF ~ HYM	Agrees
		Duluth, MN	AHYM ~ AHYF	Agrees
		Hawk Cliff, ON	AHYM ~ AHYF	Agrees
		Hawk Mt., PA	AHYM ~ AHYF	Agrees
		Cape May, NJ	AHYM ~ AHYF	Agrees
	Kjellén 1992	Sweden	AHYM > AHYF	AHYM ~ AHYF
		Sweden	HY > AHY	AHY > HY
Northern Goshawk	Kjellén 1992	Sweden	HYM ~ HYF	Agrees
Cooper's Hawk	Duncan 1981	Hawk Cliff, ON	(HYM > HYF)[c]	Agrees
			(AHY > HY)	Agrees
			AHYM > AHYF[d]	AHYF>AHYM
	Delong & Hoffman 1999	Goshutes, NV & Manzanos, NM	AHYM>AHYF	AHYF>AHYM
			AHY > HY	Agrees
			HYM > HYF	Agrees
Sharp-shinned Hawk	Rosenfield & Evans 1980	Duluth, MN	(AHY > HY)	Agrees
			(M > F)	Agrees
	Duncan 1982	Hawk Cliff, ON	AHY > HY	Agrees
			M > F	Agrees
	DeLong & Hoffman 1999	Goshutes, NV & Manzanos, NM	AHY > HY	Agrees
			M > F	Agrees
Red-tailed Hawk	Haugh 1972	Hawk Cliff, ON	(AHY > HY)	Agrees
	Brinker & Erdman 1985	ne. WI	(AHY > HY)	Agrees
	Geller & Temple 1983	Cedar Grove, WI	(AHY > HY)	Agrees
	Kessel & Springer 1966	cent. AK	(HY > AHY)	AHY > HY
Red-shouldered Hawk	Dunne & Clark 1977	Cape May, NJ	(AHY > HY)	Agrees
	Field & Field 1979	Hawk Cliff, ON	(AHY > HY)	Agrees
Rough-legged Hawk	Kjellén 1992	Sweden	HY > AHY	HY ~ AHY
American Kestrel	Haugh 1972	Hawk Cliff, ON	(M > F)	Agrees
	Smallwood 1988	s. cent. FL	AHY > HY	Agrees
Merlin	Clark 1985a	Cape May, NJ	(M > F)	Agrees
	Kjellén 1992	Sweden	AHYM > AHYF	Agrees
			HY > AHY	AHY > HY
Peregrine Falcon	Hunt et al. 1975	Texas coast	HY > AHY	Agrees
			F > M	Agrees
	Berry 1971	Assateague I., MD	(HY > AHY)	Agrees
	Ward et al. 1988	Assateague I., MD	HY ~ AHY	HY > AHY
			F > M	Agrees
	Kjellén 1992	Sweden	HY > AHY	Agrees

[a] ~ indicates no significant difference.

[b] > indicates significantly later than ($P < 0.05$).

[c] No statistics were performed on entries in parentheses.

[d] Statistics performed by us.

addition to Newton's (1979) suggestion that adult long distance migrants might come into condition for migration sooner than juveniles, Kjellén (1992) proposed that adults might leave early so that more food would be available for the young, and the early arrival of the adults on the wintering area would permit acquisition of a good territory. A good winter territory would permit rapid completion of molt and accumulation of energy reserves for spring migration and the next breeding season. Adults also migrated before juveniles in 5 short distance migrants at Falsterbo. Kjellén (1992) argued that the main advantage to adults is the same as for long distance migrants: a better chance to secure a good winter territory. Juveniles migrated before adults in two short distance migrants, and Kjellén (1992) believed this is because a large part of the adult population winters close to the breeding grounds in Scandinavia, and adults either displace the juveniles or the latter are less able to cope with the reduced prey available in winter. Kjellén (1992) was unable to offer an explanation for the one remaining species (Marsh Harrier) because all individuals leave Scandinavia for southern Europe and Africa, but juveniles migrate before adults.

Our analysis of Kjellén's (1992) data fails to show relationships between which age group migrates first and the maximum distance of migration (Table 1; Mann-Whitney $U_{8,3} = 16$, $P > 0.05$), the northern ($U_{8,3} = 11$, $P > 0.05$), or the southern ($U_{8,3} = 12$, $P > 0.05$) limits of the wintering range. Adults migrate earlier than juveniles in species that breed farther north ($U_{8,3} = 2$, $P = 0.04$). The differences between Cedar Grove and Falsterbo in the timing of migration of adults and juveniles can also be explained by the northernmost latitude of breeding. Falsterbo is more than 12° latitude (about 1300 km) north of Cedar Grove and only 4 of the 10 species at Cedar Grove breed north of the latitude of Falsterbo. The relationship between maximum breeding latitude and adults preceding juveniles in Cedar Grove and Falsterbo combined is highly significant ($U_{9,11} = 2$, $P < 0.001$).

Two species occurring at Cedar Grove breed at higher latitudes than any species at Falsterbo. Peregrine Falcon adults migrate before juveniles, but there is no age difference in the timing of migration in the Rough-legged Hawk. The best explanation for early migration of adults is probably our suggestion of an early departure and more rapid migration of the adults.

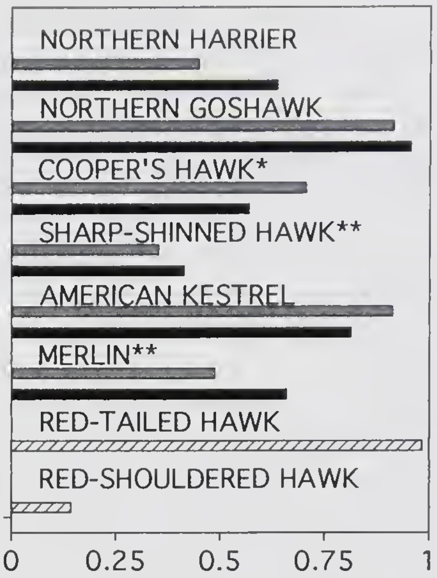

FIG. 2. Proportion of hawks with incomplete molt of remiges of rectrices during fall migration. Black bars: females. Shaded bars: males. Hatched bars: unsexed. Sex difference significant *$P < 0.05$. **$P < 0.01$.

Sex differences in the timing of migration.—In our study, males migrated significantly later than females in 13 of 22 possibilities, females significantly later than males in 4, and there was no significant difference between the sexes in 5 cases. Therefore, the two hypotheses that predict earlier migration of males (the social dominance and body size hypotheses) are rejected. The feeding efficiency hypothesis predicts that females migrate earlier because they are less efficient predators than males and must migrate with most of their avian prey. This hypothesis can apply to only a few species because birds are a minor component in the diet of most species. The molt hypothesis predicts that adult males migrate later than adult females but makes no prediction about juveniles. Juvenile females migrate significantly earlier than juvenile males in 7 of 10 species and adult males later than adult females in only 4 of 10 species. Incomplete molt of the remiges and rectrices was significantly more common in females than in males in 2 species (Fig. 2). Incomplete molt was significantly more common in males in only 1 species. Overall, there is little support for the molt hypothesis.

Females migrated significantly later than males in ASY Northern Goshawks and Cooper's Hawks. Newton (1979) noted that whether males or females stay on the breeding area seems to correlate with which sex is most attached to the territory; this appears to be the female in at least some species of *Accipiter*. The nesting territory of the Northern Goshawk is established and maintained by the female, and the same might be true of the Eurasian Sparrowhawk (Cramp and Simmons 1980).

We hypothesize that prolonged occupancy of the territory in autumn provides an advantage the following breeding season with the greatest advantage accruing to the sex that is the primary defender of the territory. This is usually the male but in the larger species of *Accipiter*, it appears to be the female. Several observations are consistent with the hypothesis that occupancy and defense of breeding territory are the rationale for late migration in fall. The mean difference and SD in median date of migration between the sexes in juveniles is 3.0 ± 1.73 days and for adults it is 5.9 ± 3.85 days. The difference between the two is nearly statistically significant (Wilcoxon matched-pairs signed-ranks test: $Z = 1.89$, $P > 0.05$). The mean difference in the median date of migration between adults and juveniles is 17.3 ± 10.56 days, which differs significantly from the differences between sexes in juveniles (Mann-Whitney $U_{7,7} = 4.5$, $P = 0.01$) and adults ($U_{7,7} = 9$, $P = 0.05$).

Except perhaps the American Kestrel, most individuals of most species of the raptors considered in this study probably do not breed until they are two years old (Palmer 1988). Thus, there is no reason for juveniles to delay their fall migration to occupy territories. Juvenile males migrated significantly later than juvenile females in 7 of 10 species at Cedar Grove, including the Cooper's Hawk, whose adult females migrate significantly later than adult males. Juvenile males migrate significantly earlier than juvenile females only in the Peregrine Falcon. We suggested that this species leaves the arctic breeding ground as soon as possible. Young male Peregrine Falcons fledge a mean of 3.5 days earlier than females (Sherrod 1983), and males migrate a mean of 2.3 days earlier than females.

Our results on sex differences differ from those of other studies in only 4 of 25 comparisons (Table 2). HY female Northern Harriers migrated significantly later than HY males at Cape May, but there was no significant difference at Cedar Grove. AHY male Northern Harriers migrated significantly later than AHY females at Falsterbo, but the difference was only marginal at Cedar Grove. AHY female Cooper's Hawks migrated significantly later than AHY males at Cedar Grove, and the opposite is true at Hawk Cliff, the Goshutes, and the Manzanos. We have no explanation for the significant disagreement between our results and those from Hawk Cliff, the Goshutes, and Manzanos.

Sex and age differences in wintering areas.—Several of the hypotheses predict age or sex differences in wintering distributions. Only a few Northern Harriers, all adult males, winter in central Wisconsin (Hamerstrom 1969). Adult males are disproportionately common around the northern Gulf of Mexico in winter (Palmer 1988). The evidence is thus inconclusive. Clark (1985b) indicated that female Sharp-shinned Hawks banded as migrants at Cape May, New Jersey, tended to winter farther north than males, but the opposite was true of birds banded at Duluth, Minnesota (Evans and Rosenfield 1985); however, an analysis of their data showed that the differences between sexes are not significant (Mann-Whitney $U_{28,73} = 1153$, $P > 0.05$, $U_{12,15} = 73$, $P > 0.05$ respectively). Although Clark (1985b) did not comment on age differences, an analysis of his data showed that there were no significant differences in the latitudinal distribution of recoveries ($U_{86,15} = 597$, $P > 0.05$). We analyzed the distributions of Sharp-shinned Hawks banded at Cedar Grove and recovered between 9 November and 15 March: 18 adult females recovered at a mean latitude of 32°, 15 juvenile females at 34°, 14 adult males at 33°, and 6 juvenile males at 31°. There are no significant differences between sexes ($U_{20,33} = 271$, $P > 0.05$) or between juveniles and adults ($U_{30,23} = 321$, $P > 0.05$).

Brinker and Erdman (1985) concluded that adult Red-tailed Hawks wintered in more northerly locations than juveniles, but an analysis of their data shows that the trend is not significant ($U_{24,33} = 345.5$, $P > 0.05$). Gauthreaux (1985) analyzed the distributions of museum specimens and found that female Rough-legged Hawks wintered significantly farther north than males. Our data suggest that males migrate later than females, which is inconsistent with males wintering farther south. Based on 152 Christmas Bird Counts, female American Kestrels wintered significantly farther north than males (Arnold 1991). Females were significantly more abundant than males in winter in Florida, and females were significantly more abundant in the southern part of the state than in the northern part (Layne 1982). Other reports also suggest that males are more common in the northern parts of the wintering range (Mills 1975, 1976; Enderson 1960). These results are consistent with our finding that females migrate earlier than males.

The following hypotheses best explain our findings of age and sex differences in the timing of fall migration. Adults migrate before juveniles in species that breed at high latitudes because the breeding season is short and adults probably leave as soon as the young can care for themselves. The adults apparently also migrate faster than juveniles. In species breeding in more temperate latitudes, adults migrate later than juveniles because of a presumed advantage gained from remaining on territory as long as feasible. The sex that migrates later (usually the male) is the sex primarily responsible for territorial defense.

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NESTING HABITAT AND SUCCESS OF THE CHIMANGO CARACARA IN SOUTHERN CHILE

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ABSTRACT.—We studied the nesting ecology of the Chimango Caracara (*Milvago chimango*), a common yet poorly known raptor on Chiloé Island, southern Chile, during two breeding seasons. Deforestation and land clearing in this landscape may be benefiting this raptor, which is tolerant of open and disturbed habitats and human activity. Chimangos nested at different heights in a variety of trees and shrubs, but nests were always well concealed because they were placed centrally and in dense vegetation within the substrate. Egg laying occurred in most nests in October during both years; the most common clutch sizes were 2 or 3 eggs. The incubation and nestling periods were approximately 5 (2 nests) and 6 (1 nest) weeks, respectively. Nest success (Mayfield) for 72 nests averaged 57% for the two years. Productivity averaged 1.22 ± 0.11 fledglings per active nest and did not differ between years. For nests located during both years ($n = 15$), productivity was slightly higher in 1997–1998 and more nests failed in 1998–1999. Two pairs attempted to renest after nest failure but were not successful. Habitat and landscape features associated with high productivity of chimango nests included exotic trees and shrubs, tidal flats, linear forest strips, and occupied houses or barns. Successful nesting was associated with exotic trees and shrubs. Nesting density was highest along beaches, although not all pairs that built nests along beaches laid eggs. Successful nests along beaches fledged twice as many young as inland nests. Continued clearing of the rainforest in this region may provide increased foraging opportunities for this raptor but may also result in fewer nest sites. *Received 6 July 1998, accepted 24 Dec. 1999.*

The Chimango Caracara (*Milvago chimango,* Falconidae, Caracarinae) is a common raptor in southern South America (Brown and Amadon 1968, del Hoyo et al. 1994). The chimango occurs in both forested and open habitats throughout its range and is frequently found around human settlements. This generalist predator has a varied diet, which includes carrion and human refuse as well as live prey such as insects, worms, and other invertebrates, small mammals, and nestling birds (Johnson 1965, Yáñez et al. 1982).

The temperate rainforest in South America is restricted to southern Chile and adjacent western Argentina and, as such, functions as an ecological island (Vuilleumier 1985). The associated avifauna is comprised of numerous endemic species, many of which are increasingly threatened by forest fragmentation (Balmford and Long 1994, Willson et al. 1994). In many areas, expanding anthropogenic influences are transforming landscapes into patchworks of different sized forest fragments interspersed with pastures and crop fields interconnected with linear forest strips (Willson et al. 1994).

Clearing of the forest in many areas is likely to be advantageous for open habitat species such as the Chimango Caracara. The chimango apparently is tolerant of human activity (Jaksic and Jiménez 1986), and farms augment the chimango's food resources, providing poultry and earthworms. Consequently, the chimango may be benefiting from forest fragmentation by numerically responding to increases in the amount of open area resulting from forest clearing. A known predator on eggs and nestling birds (Fraga and Salvador 1986; Donázar et al. 1996; K. Sieving and M. Willson, unpubl. data), the chimango may represent an increasing threat to endemic forest birds confined to remnant forest patches and strips.

The ecology of the chimango is poorly known. Its breeding biology and nesting habitat in Argentina have been described (Fraga and Salvador 1986, Travaini et al. 1994), but the overall paucity of information on the species limits our ability to evaluate its response to land use changes or its potential role as a nest predator. Here, we report data collected during two breeding seasons on the nesting habitat and nest success of the Chimango Caracara in southern Chile.

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STUDY SITE AND METHODS

We studied the Chimango Caracara on private farms throughout northeastern Isla Grande de Chiloé, Region X, southern Chile (43° 55′ S, 73° 35′ W). The study area, approximately 24,000 ha, extends from the western to the eastern coasts of the island. Agriculture is the primary land use, resulting in a landscape that is a diverse mosaic of forest patches and linear strips, fields containing scattered secondary growth of trees and shrubs, open pastures, and agricultural fields. Remnant patches of forest are greatly disturbed by logging, removal of firewood, and cattle grazing; patch sizes range from less than one to several hundred hectares. Species in the canopy are broad-leaved evergreen trees. Dominant trees in these second-growth forests include canelo (*Drimys winteri*), notro (*Embothrium coccineum*), mañio (*Podocarpus nubigena*), arrayan (*Luma apiculata*), luma (*Amomyrtus luma*), and meli (*A. meli*). Scattered trees characteristic of the original primary rainforest include coigue (*Nothofagus nitida*), ulmo (*Eucryphia cordifolia*), and tepa (*Laureliopsis philipiana*). The forest understory contains few shrubs, although species of quila (*Chusquea* spp., arborescent bamboos) and tree ferns (*Lophosoria quadripinnata*) occur frequently; the bamboos form dense thickets. Shrubs, found primarily along forest edges and in open fields, include *Rhaphithamnus spinosus*, species of *Fuchsia*, *Pernettya*, and *Berberis*, and the exotic pest, gorse (*Ulex europea*). Pastures and open fields contain a variety of pasture grasses and forbs. Common trees around dwellings and cultivated areas include exotic species such as Douglas fir (*Pseudotsuga menziesii*), cypress (*Cupressus* spp.), and pine (*Pinus* spp.). The climate is temperate and humid. Annual rainfall averages 2000–3000 mm; more than one third of the total falls during the summer warm season (December through March). Air temperatures range from 5–25° C in summer and from 2–15° C in winter.

During October 1997 through January 1998 (Year 1) and again in October 1998 through January 1999 (Year 2), we searched for nests in areas where we observed chimangos. Once found, nests were checked weekly to monitor status. Nests were classified as active (with at least 1 egg laid) or inactive (where new material was added but no eggs or young were ever observed). We examined nest contents and determined clutch size, brood size, and chick age using a mirror attached to an extendible pole or by climbing the nest tree.

To evaluate breeding chronology, we divided each month into two periods, early and late (1–15 and 15 to end, respectively). We assigned clutch initiation for each of the sample nests to one of these periods, based either on the known time of egg-laying or on back dating from known hatching or fledging dates. We continued to check breeding areas with nest failures for signs of renesting.

We estimated overall nest success using Mayfield's method (Mayfield 1961, Johnson 1979) and estimated weekly nest success probabilities separately for the incubation and nestling periods. We defined a successful nest as one in which at least one chick fledged. At some nests, older chicks were observed perched on branches away from the nest; we assumed that these chicks successfully fledged. We compared nest success probabilities using the program CONTRAST (Sauer and Williams 1989). Productivity was measured as the number of young fledged per active nest.

To characterize the chimango's nest sites, we recorded substrate species, substrate height, nest height, and nest orientation (compass direction) and position (central or peripheral) within the substrate for each nest found. We tested the hypothesis of no directional orientation of nests within the substrate using Rayleigh's test (Batschelet 1981). We also estimated canopy cover above each chimango nest and measured linear distances between neighboring nests.

We analyzed associations between reproductive success of the chimangos and particular habitat or other features characteristic of this human dominated and diverse landscape. From radiotelemetry, we determined that breeding chimangos generally forage within 250 m of their nest (J. Morrison, unpubl. data). For this analysis, we recorded presence or absence of certain features within 250 m of each nest we found and considered these features to be accessible to the pair occupying that breeding area. Features included: small (less than 1 ha in size) and large (>50 ha) forest patches, linear forest strips (<50 m in width), pasture, cultivated agricultural fields, exotic trees or shrubs, human activity (occupied house or barn), freshwater streams or marshes, and tidal flats.

We examined the association of reproductive success with the presence or absence of these features within 60 chimango breeding areas. Although some of the breeding areas were known both years, we used only reproductive success information for the first year in which the area was identified and a nest was found. We calculated two indices of reproductive success for each breeding area: (1) nesting success (succeeded or failed) and (2) productivity (high or low). We considered nests that fledged 2 or 3 young as having high productivity; nests with low productivity fledged only one chick or failed. We used 2 × 2 contingency tables and G-tests for independence with Yates' correction (Sokal and Rohlf 1995) to test relationships between presence or absence of these landscape features in the breeding areas and these two indices of reproductive success.

All results are presented as mean ± one standard error (SE) unless otherwise indicated. Statistical tests were conducted using SYSTAT (SPSS Inc. 1998).

RESULTS

We located 75 chimango nests in 60 different breeding areas during the two years. Because some nests were inaccessible (trees too tall or dangerous to climb) we obtained information on breeding chronology and reproductive success for only 39 and 33 nests during

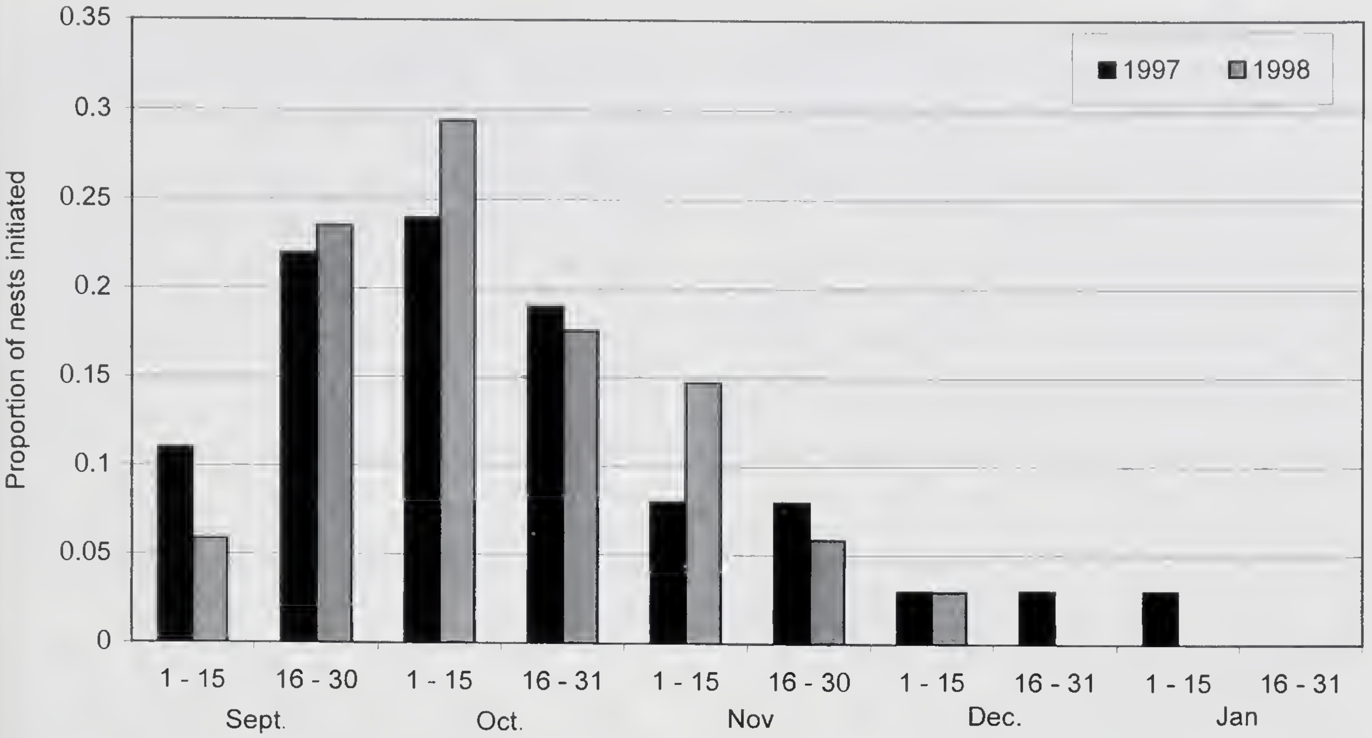

FIG 1. Initiation of egg laying in Chimango Caracara nests, Isla Grande de Chiloe, Chile, October 1997–January 1998, and October 1998–January 1999.

1997–1998 and 1998–1999, respectively. Egg-laying began in early September and peaked in early October during both years (Fig. 1). Overall, clutch size averaged 2.30 ± 0.17 (range = 1–3 eggs) and did not differ between years ($t = -0.76$, $P > 0.05$; Table 1). Each year, similar proportions of nests contained 2 and 3 eggs and only 1 nest contained a single egg (average 11% of nests). Hatching rate averaged 84% (Table 1). Overall probability of nest success to fledging for the two years was 0.57 ± 0.04 (SD) but was higher in 1998–1999 ($\chi^2 = 9.76$, $P < 0.01$; Table 1). Success estimates differed between the incubation and the nestling periods during 1998–1999 ($\chi^2 = 11.8$, $P < 0.001$) but not during 1997–1998 ($\chi^2 = 0.26$, $P > 0.05$; Table 1). Productivity averaged 1.22 ± 0.11 young per active nest and did not differ between years ($t = -0.53$, $P > 0.05$). For nests known during both years ($n = 15$), productivity was slightly higher ($t = 2.13$, $P = 0.05$) in 1997–1998 (1.77 ± 0.21) than in 1998–1999 (1.11 ± 0.20), and more nests failed in 1998–1999

TABLE 1. Reproductive parameters for Chimango Caracara (*Milvago chimango*) nests, Isla Grande de Chiloé, Chile during 1997–1998 and 1998–1999. Results are presented as mean and (SE) unless otherwise indicated.

	1997	1998
Total nests followed	39	33
Number of nests that successfully hatched eggs	34	30
Number of nests that successfully fledged young	28	24
Clutch size	2.38 (0.18) (n = 13 nests)	2.14 (0.26) (n = 7 nests)
Mayfield nest success probabilities (SD)		
Incubation period	0.67 (0.05)	0.73 (0.05)
Nestling period	0.70 (0.03)	0.91 (0.02)
Overall to fledging	0.47 (0.04)	0.67 (0.05)
Number fledged per territorial pair	1.26 (0.16)	1.15 (0.13)
Nest failures (%)	11 (28%)	9 (27%)

(17% vs 6% in 1997–1998). We found evidence of two renesting attempts after failure, both nests subsequently failed. In other cases where nests apparently failed, the adults remained around the nesting area, but we found no evidence of renesting.

Both sexes participated in nest-building, incubation, feeding the young, and defending the nest. The incubation and nestling periods were approximately 32 ($n = 2$) and 41 ($n = 1$) days, respectively. Pinfeathers were first visible on chicks at about 2.5 weeks of age. At about 5 weeks of age, chicks began to perch away from the nest on other branches in the nest tree. If flushed from the nest at this age, chicks flew readily and fairly easily among trees and rarely came to the ground.

Chimangos nested ($n = 75$ nests) in a variety of sites including dense forest (13%), the right-of-way of a major road (15%), open habitat containing scattered trees, shrubs, or scrubby vegetation (53%), within 100 m of an occupied house or barn (45%), and along beaches, generally also near an occupied house or barn (15%). Chimangos used a range of nesting substrates of varying heights, including native and exotic trees and shrubs, and snags (mean substrate height 12.2 m ± 0.8, range 3.4–28.9 m, $n = 75$ nests; Table 2). Chimangos tended to place their nests near the central part of the substrate (69% of all nests) and under dense canopy cover (71.8% ± 2.7, $n = 73$ nests; Table 2). Nests showed a slight directional orientation but angular dispersion was high (mean = 63°, Rayleigh's R = 15.61, $s = 101°$, $n = 74$, $P < 0.05$; Table 2).

Breeding chimangos exhibited behaviors typical of other territorial raptors. They were highly aggressive near the nest and pairs often stooped and attacked us when we climbed nest support structures. Other chimangos in particular were attacked and rapidly chased away from the nesting area. Despite this apparent intolerance of conspecifics, we found chimango pairs nesting quite close together at some sites. Adjacent pairs nested closer together ($t = -2.40$, 17 df, $P = 0.03$) along beaches (170 m ± 30 m, range = 60–180 m, $n = 5$ pairs) than inland (470 m ± 70 m, range = 40–1070 m, $n = 14$ pairs). At one beach site, we found 3 pairs building nests in a line of exotic cypress trees approximately 100 m in length. Only one of these pairs successfully raised chicks. The other pairs never laid eggs, although they remained in the area and continued adding nest material to the structures through January.

Tests of association between landscape features and productivity indicated that high productivity (29 of 60 nests) was positively associated with exotic trees or shrubs, linear forest strips, and tidal flats and perhaps with human activity (Table 3). Productivity in breeding areas along beaches (2.14 ± 0.26, $n = 9$) was higher ($t = 3.48$, 12 df, $P < 0.01$) than productivity of inland breeding areas (1.06 ± 0.17, $n = 51$). Successful nesting was associated with exotic trees and shrubs (Table 3).

DISCUSSION

The chimango is the most common bird of prey on Chiloé, perhaps in all of Chile. It can be observed regularly in all habitats and particularly in those occupied by humans. Large groups of chimangos (>50) were often seen along beaches, in pastures, and on edges of towns.

Breeding chronology of chimangos in our study area was similar to that reported for chimangos nesting in Argentina (Fraga and Salvador 1986). In their study areas in Buenos Aires and Córdoba provinces, Fraga and Salvador (1986) found nests with eggs from the end of September through December with a peak of egg laying in October. They also reported larger mean clutch sizes (2.76 ± 0.43) but a shorter incubation period (26–27 d) for chimangos nesting in their study areas than we noted for chimangos nesting on Chiloé. Fraga and Salvador (1986) reported nest success of 30% for chimangos in their study area and indicated that many nests were lost to predation.

Weather on Chiloé can be inhospitable and undoubtedly has played an important role in the evolution of the chimango's reproductive biology. The chimango's low nest success on Chiloé may be attributed to wind and rainstorms which are common on Chiloé and may cause nest failures. Nest failure also could be due to nest predation, perhaps by conspecifics. We regularly observed territorial behavior by breeding pairs, including 4 or more chimangos chasing and fighting within breeding areas, often near active nests.

TABLE 2. Summary of nest site characteristics for 75 Chimango Caracara (*Milvago chimango*) nests, Isla Grande de Chiloé, Chile, 1997–1999. Values are mean and (SE).

Tree species	*n* nests	Substrate height (m)	Nest height (m)	Nest position relative to substrate top (%)	Nest orientation (°)	Nest position within substrate[a]	Canopy coverage above nest (%)
Acacia melanoxylon[b]	1	7.9	6.4	81	100	1	55
Amomyrtus luma	2	9.4 (1.5)	8.4 (1.9)	88 (0.1)	185	1-1, 1-2	77.5 (17.5)
Aracaria araucana	1	13.7	13.1	96	218	2	60
Cupressus spp.[b]	9	22.0 (1.8)	14.9 (1.9)	68 (0.1)	54	4-1, 5-2	71.1 (7.3)
Drimys winteri	2	9.3 (0.2)	8.4 (0.2)	90.0 (0.0)	48	1-1, 1-2	65 (5.0)
Eucryphia cordifolia	6	10.8 (1.5)	9.6 (1.4)	88.0 (0.0)	274	2-1, 4-2	81.3 (8.5)
Laureliopsis philipiana[c]	2	13.9 (2.6)	9.1	81	278	1-1, 1-2	45 (0.0)
Luma apiculata	10	8.6 (1.2)	7.3 (1.2)	82.0 (0.0)	135	3-1, 7-2	66.5 (8.4)
Malus bacatta[b]	1	9.1	7.3	80	170	1	40
Pilgerodrendron uviferum	1	3.4	2.3	68	75	1	25
Pinus spp.[b]	8	21.4 (1.8)	16.5 (2.0)	77 (0.1)	68	2-1, 6-2	67.5 (9.2)
Podocarpus nubigena	15	8.1 (0.7)	7.0 (0.7)	86.0 (0.0)	66	12-1, 3-2	83.5 (4.8)
Pseudotsuga menziesii[b]	8	13.3 (1.2)	10.4 (0.9)	78.0 (0.0)	166	7-1, 1-2	87.3 (5.0)
Rhaphithamnus spinosus	7	6.6 (1.0)	4.7 (0.8)	70.0 (0.0)	161	2-1, 5-2	61.4 (6.4)
snag, species not known	2	9.3 (1.7)	7.9 (0.9)	86.0 (0.1)	310[d]	—	50[e]

[a] Nest position: 1 = central to the substrate, such as along the main stem or trunk; 2 = peripheral within the substrate, such as out on a branch away from the main stem or trunk.

[b] Exotic species.

[c] One nest tree of this species was in dense forest, thus we could not measure variables other than substrate height.

[d] Measured for 1 nest only. The other nest was in the open, broken top of the snag so nest orientation and nest position within substrate were not measurable.

[e] Canopy cover for the nest inside the snag was 100%, for the nest in the broken top snag, 0%.

TABLE 3. Results of tests of association between landscape features and indices of reproductive success of Chimango Caracaras on Isla Grande de Chiloé, Chile. The total number of nests used for this analysis was 60; *n* is the number of breeding areas having each variable.

Feature	*n*	Nest productivity *P*	Nest success *P*
Small forest patch	37	>0.05	>0.05
Large forest patch	8	>0.05	>0.05
Pasture	58	>0.05	>0.05
Exotic trees or shrubs	30	<0.01	<0.01
Cultivated agricultural fields	29	>0.05	>0.05
Human activity	50	>0.05	>0.05
Freshwater streams or marshes	21	>0.05	>0.05
Tidal flats	9	0.01	>0.05
Linear forest strips	42	0.04	>0.05

While successful nesting by chimangos in this landscape could be associated with features other than those we measured, we believe that the apparent lack of association between most of these features and successful nesting as shown by our results further suggests nest predation as a potential cause for nest failure in this population.

Although nest success estimates for chimangos in our study area were higher than estimates reported by Fraga and Salvador (1986), actual nest success of chimangos on Chiloé may be lower than our results suggest. Of nests known during both years, more failed in 1998–1999 than in 1997–1998, perhaps suggesting that we mostly found successful nests. We could have missed nests that failed during egg laying or early in the incubation period, particularly if predation risk to nests is high.

Although we did not find chimangos nesting on the ground as has been reported elsewhere (Fraga and Salvador 1986, Travaini et al. 1994), chimangos on Chiloé nested in a wide variety of sites and often near human activity. Heights of substrates used for nesting by chimangos in our study area were taller on average than those reported elsewhere (Fraga and Salvador 1986, Travaini et al. 1994). This difference may reflect the availability of different woody species as potential nesting sites on Chiloé, particularly exotic trees such as cypress and pine. Although we found a significant orientation in the direction of the nests, as did Travaini and coworkers (1994), we also observed a great deal of scatter. Chimangos on Chiloé tended to nest near the protected, central place of the substrate and under dense canopy cover. Such placement may provide maximum protection from inclement weather and may also reduce predation risk.

We did not observe semicolonial nesting of chimangos on Chiloé as has been reported elsewhere (Fraga and Salvador 1986); however, we found pairs nesting as close together as 40 m in some areas, particularly along beaches. Fraga and Salvador (1986) suggested that semicoloniality of chimangos at their study sites was due to spatial and temporal variation in food resources rather than lack of nest sites. On Chiloé, high nest productivity and nesting density along beaches suggest that these areas provide good habitat and abundant food resources for the chimangos.

The wide variety of nesting sites used by chimangos on Chiloé may be a consequence of a high density of this species in the study area or a lack of specific nesting requirements. Conversely, it could be argued that continued clearing of land for housing and farms on Chiloé may be resulting in loss or altered availability of nest sites for the chimangos. Selection for a particular nesting situation may be obscured by habitat saturation or nest site limitations that would restrict nesting possibilities. Especially along beaches, competition for both nest sites and food was suggested by the fact that some pairs built nests but never laid eggs and by frequently observed chasing and fighting among pairs.

Studies have shown that the density of generalist predators increases as a forested landscape becomes fragmented and interspersed with agricultural land (Whitcomb et al. 1981, Andrén 1992). Our results suggest some association between high productivity and success of chimango nests and features that reflect the human presence in the current landscape on Chiloé including exotic trees and shrubs, linear forest strips, and occupied houses or barns. The thick branches and dense crowns of exotic trees such as cypress and pine may provide better protection from weather or from predators, perhaps explaining the association of this variable with successful nesting. Around human dwellings exotic trees and shrubs are often the only species present because most of the landscape has been cleared for pasture or crops. Rather than reflecting selection for these exotic species, their use by nesting chimangos instead may reflect the availability of suitable nest sites or selection of a site near food sources (farms). The association of forest strips with high nest productivity may reflect the proximity of these strips to pasture. Alternatively, forest strips have relatively large amounts of edge and thus may provide more foraging opportunities for the chimangos, which are known to prey heavily on bird nests in edge habitats (M. F. Willson, J. L. Morrison, K. E. Siving, T. L. De Santo, L. Santistehan, and I. Díaz, unpubl. data).

The chimango caracara is a generalist predator associated with landscapes impacted by humans. On Chiloé, the chimango's apparent tolerance of humans, generalist diet, and use of open habitats may increase the species' potential both as a nest predator on forest birds and as a pest to local landowners. Continued forest clearing and expansion of human activity on Chiloé will likely improve foraging opportunities for the chimango. Conversely, continued clearing of land may lead to increased competition for nest sites or higher predation on chimango nests.

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Announcement

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PARENTAL CARE OF FLEDGLING WOOD THRUSHES

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ABSTRACT.—We report the study of parental care of Wood Thrush (*Hylocichla mustelina*) fledglings from nest-leaving to independence. From 1993 to 1995, we captured, radio-tagged, and monitored the movements and behavior of 23 fledglings and their parents from 12 broods at the U.S. Marine Corps Base, Quantico, Virginia. For pairs that subsequently renested (n = 5), the family group of male, female, and fledglings, remained within 62 (±5 SE) m of the first nest after fledging. During the period of post-fledging parental care, mean maximum distance between parents was 70 (±14) m. Females attended the young 13 (±1.3) days before initiating the incubation of a second clutch. Males continued attending the fledglings for 6 (±0.7) more days until the young achieved independence and dispersed (28–36 days post-hatching). In final clutches (n = 7), brood care was divided between the parents, and the position of the fledglings relative to the nest depended on the parents' choice of molting site (in the nesting area or elsewhere). Division of the brood by the parents has been thought to be a strategy to reduce predation and increase foraging efficiency. However, in the Wood Thrush and other species, joint attendance of initial broods, but division of final broods, suggest that other factors could be important for the parents' decision of whether or not to split the brood. *Received 15 June 1999, accepted 13 Nov. 1999.*

Parental care in passerines is not restricted to the nestling stage, but extends beyond fledging. In fact, the duration of parental care after fledging of the young can be as long as that of the nestling period (Skutch 1986), and investment by the parents may be even greater during this phase than during the nestling stage (Drent and Daan 1980, With and Balda 1990). Therefore, documentation of postfledging dependence events is important not only for understanding parental investment patterns and mating systems, but also for understanding its role in reproductive success and population demography (Royama 1966, With and Balda 1990). Difficulties in observing the young after they have left the nest has limited the gathering of information on this stage of the life cycle (Weatherhead and McRae 1990).

The Wood Thrush is a relatively well-known species, but little has been published on the postfledging, pre-independence phase of its life cycle. Roth and coworkers (1996) devoted only one paragraph to this stage, and scattered observations are found in Brackbill (1958) and Anders and coworkers (1997). We reported elsewhere on movements of young following independence (Vega Rivera et al. 1998). In this paper we report the behavior of adult Wood Thrushes (*Hylocichla mustelina*) and their young from fledging until the young reach independence. Our main objective is to provide information on development of the young and on parental care during the post-fledging, pre-independence period. Specifically we report the extent to which the male and female parents were involved in the care of fledglings and how this behavior was affected by the status of the parents attending early or late broods.

STUDY AREA AND METHODS

We conducted the study at the Marine Corps Base (MCB), Quantico, Virginia (38° 30′ N, 77° 25′ W, area 243 km^2). Native forest types cover about 75% of the base and are stands of Virginia pine *Pinus virginianus* (17%) and mixed forest (83%). Details of the study area and methodology can be found in Vega Rivera and coworkers (1998).

During the summers of 1993–1995, we captured, radio-tagged, and monitored the movements and behaviors of 23 fledglings and their parents from 12 broods. Nests were found by tracking adults that were previously captured and radio tagged and by checking likely nest sites. We radio tagged the offspring 2–3 days before they fledged. Transmitters (Model BD-2G, Holohil Systems Ltd., Ottawa, Canada; average life >120 days; range of detection 400–1000 m on the ground) were attached using a leg backpack-harness (Rappole and Tipton 1991). Radio-tagged birds were located every other day. Once a bird was located, we continuously monitored its behavior for up to 30 minutes. We recorded the type of substrate (ground, bush, tree),

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height of perch, spatial separation of young and parents, and interactions between parents and young. Individual and nest locations were recorded using a GIS generated map of the Marine Base and a global positioning system (Pathfinder Pro GPS, Trimble Navigation Ltd., Sunnyvale, California). A minimum of 75 fixes were obtained for each location, which were differentially corrected and averaged using PFINDER software, and entered as a coverage into the base's GIS database.

We defined initial broods as those followed by another nesting attempt and final broods as those with no subsequent nesting attempt. Age is given as the number of days after hatching, with day 1 as the day the nestling hatched. Day of hatching was extrapolated from laying dates using 13 days as an averaged incubation period (Roth et al. 1996; pers. obs.). We regarded fledglings as independent when no further parent-offspring interactions were observed, for example, feeding of the young, flying together, alarm behavior from the parents when we approached the fledglings, or when the fledglings dispersed from the natal area without being accompanied by the parents. Values presented are means ± SE. Because young from the same nest may not be thought of as independent, distance from nest and age of independence for siblings were averaged and considered for calculations as a single data point.

RESULTS

Of 43 nests we monitored during the three years of the study (including replacements and second clutches), 25 were depredated: 5 (11.6%) during incubation, 9 (21%) at or within 1–2 days of hatching, 2 (4.2%) during the nestling period, and 9 (21%) at or within 1 day of fledging. In the remaining 18 nests (42%), at least 1 young was fledged for a total of 29 fledglings. Of these, 6 individuals (15%) were depredated within 5 days after leaving the nest. The rest (23 young or 85%) survived to independence. An account of the development of the young follows. Data for young of the same age were pooled.

Development of fledglings.—At 11 days of age, young could not fly and stayed on the forest floor. From age 12–15 days, most fledglings were able to climb bushes, but were incapable of extended flight. During this time, they often perched quietly 1–5 m above the ground, and froze when we approached them. At 16 days of age, young were able to fly at least 30 m between branches, close to the ground, or in the mid-canopy in response to parental alarm calls. By 17 days of age, most young flew proficiently, although one fledgling remained immobile for long periods at 19 days of age, while another moved very well between branches at 14 days of age.

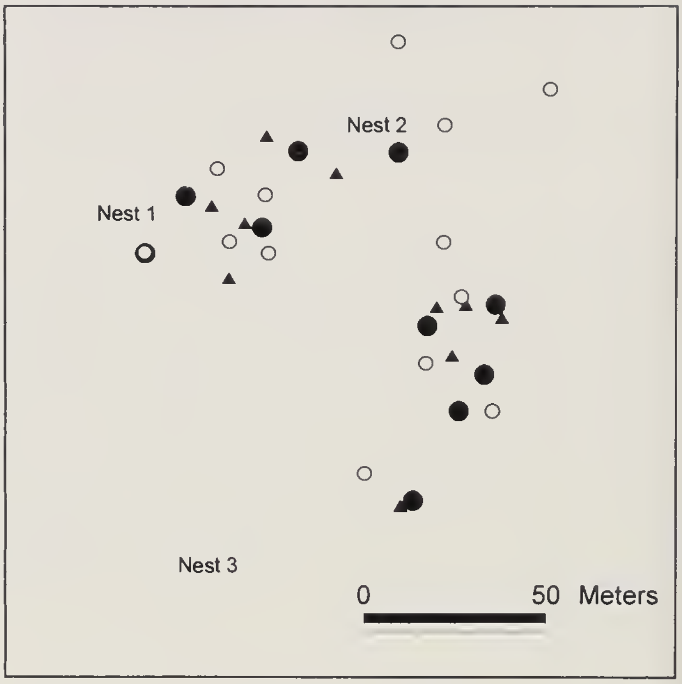

FIG. 1. Radio locations of a male Wood Thrush (○) and two fledglings (▲ and ●) from an early brood. Young were fledged from nest 1. Position of nest 2 and 3, which nestlings were depredated, are shown for reference.

We first observed fledglings feeding by themselves at 17 days of age, but it may have occurred earlier. Birds that fledged early in the season, when fruits were not available at the natal sites, foraged on the ground, often along fallen logs. Fledglings hatched later in the season, when fruits were abundant, depended heavily on fruits and spent most of the time foraging 5–10 m high in the trees.

Parental attendance and dispersal.—Adult Wood Thrushes followed one of two strategies regarding attendance of the fledglings. If the parents renested (5 pairs in our study), they kept the fledglings within 64 (±13) m of the nest (for an example see Fig. 1). Mean maximum distance between parents was 70 (±14) m. Of these pairs one had 3 young, two had 2 young, and two had 1 young. In families with more than one young, we did not notice division of the brood; both parents kept the young together and apparently attended all the young. Similarly, single young were attended by both parents. Once females started the construction of the next nest, her involvement in the attendance of the fledglings decreased and ceased altogether when they started incubation. On average, females attended the young

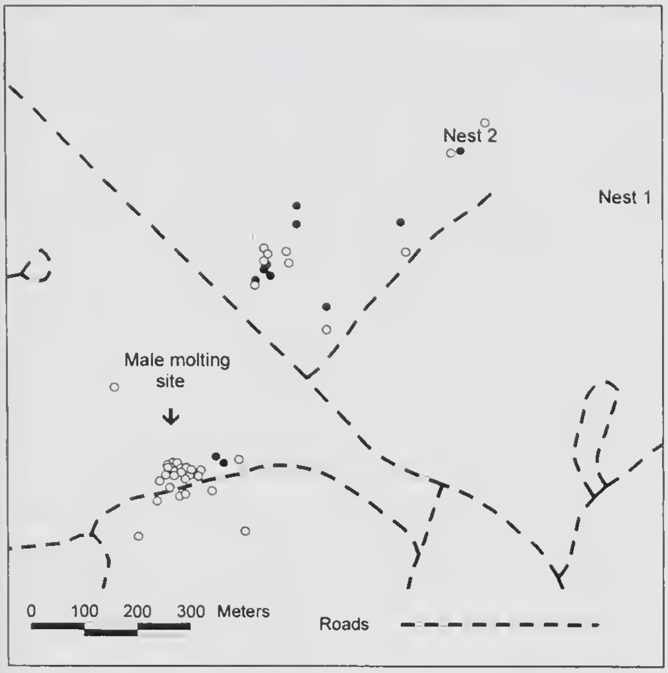

FIG. 2. Radio locations of a male Wood Thrush (○) and a fledgling (●) from a final brood on the Marine Corps Base, Quantico, Virginia. Young was fledged from nest 2. Position of nest 1, from which nestlings were depredated, is shown for reference.

13 (±1.3) days before initiating incubation of the second clutch. Once females started incubation, the males continued to attend the fledglings for 6 (±0.7) days until independence and dispersal.

In final broods (7 pairs; only 1 of these pairs successfully raised an initial brood) the strategy was different. For fours pairs, two with 2 young and two with 3 young, the brood was divided between the parents within 2–3 days of fledging with each parent subsequently feeding only specific individuals. Mean maximum distance between parents was 313 (±41) m. In two pairs, the female abandoned the study area within 4–6 days after fledgling of the young and left the male attending a single young. In a pair with two young, the male left the female attending them.

The distances that the young and the parents moved from the nest after fledging and before independence varied depending on whether the parents remained in their nesting area for molting (104 ± 5 m, n = 5 broods) or moved elsewhere (332 ± 156 m, n = 2 broods). For instance, the male of one pair with 3 fledglings moved out of the nesting territory with one of the offspring immediately after fledging, and 2 days after fledging they were more than 200 m from the nest (Fig. 2). The female remained in the vicinity of the nest site with the other two offspring.

There is no indication that fledglings from final broods become independent at an earlier age than those from earlier broods ($t = 0.02$, $P > 0.05$). Independence from parents occurred at 32.5 (±1.4, n = 5 initial broods) and 32.4 (±0.8, n = 7 final broods) days. After achieving independence, most fledglings dispersed 1.5 (±0.3) km from natal sites and joined flocks of conspecifics. There was no significant trend in direction of dispersal from the natal site (Rayleigh's Z-test: $Z = 1.51$, $P > 0.05$) nor was there a significant correlation between the distance of dispersal and date of dispersal ($r = -0.17$, $P > 0.05$). We did not note any aggression from parents toward the young or among siblings prior to dispersal. However, we observed another behavior related to dispersal of fledglings that deserves some comment. Three males, each attending a single fledgling, moved with their young out of the natal area at a time when fledglings were expected to disperse. One male and his single fledgling moved 855 m from the nesting site. The next day, the male was back in his territory, but the fledgling moved farther away. Another male and his fledgling moved 400 m from the nesting site to a second-growth area. The young stayed at that site 33 days. The male moved about 300 m from the fledgling to a deciduous sapling area and initiated molt. Similarly, a third male and his fledgling moved 500 m from the nesting site. The male returned to the nesting site 2 h later but the fledgling continued to move away.

DISCUSSION

Parental involvement during the post-fledgling, pre-independence period has been a topic of discussion because of its implications for reproductive strategies. Parents have three options regarding care of fledglings: (1) they can care for the brood together, (2) they can divide the brood with each parent providing care to a portion of the brood, or (3) one parent can care for the entire brood while the other departs or assumes other reproductive duties. We found adult Wood Thrushes employing all three strategies. Previous reports on Wood Thrush parental care mention that parents split the brood after fledging, but they remained within 200–400 m of their nests for 2–3

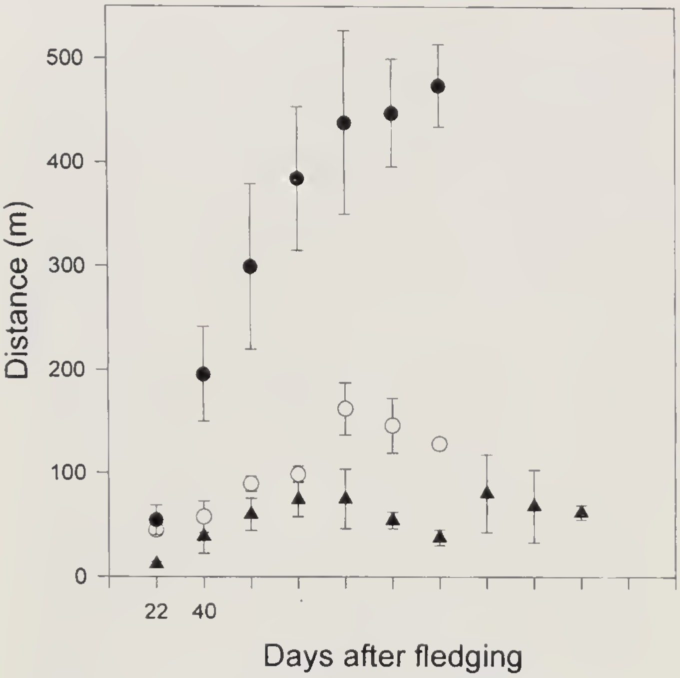

FIG. 3. Distance of young Wood Thrushes from their nests during the post-fledging, pre-independence period. ▲ represent initial nests (averaged from 5 broods); ○ represent final broods from parents that stayed in their nesting site to molt (averaged from 5 broods), ● represent final broods from parents that moved out of their nesting site to molt (averaged from 2 broods).

weeks later, while young were still attended by a parent (Roth et al. 1996). In contrast, we found that once fledglings left the nest, the distance that they moved depended on the parents' reproductive activities. If the parents were going to renest, then the entire family group (male, female, and fledglings) remained together and close to the nest. If adults had completed nesting activities for the year, then the position of the fledglings with regard to the nest depended on the parents' choice of molting site, whether on the breeding territory or elsewhere (Fig. 3).

Brood division between parents following fledging has been reported in several species of passerines and has been thought to be an advantageous strategy for reasons such as reduced predation or improved foraging efficiency (see references in Moreno 1984, McLaughlin and Montgomerie 1985). These explanations are incomplete because it is now clear that a range of post-fledging parental care patterns exist, not only for different species, but for individual pairs within the same species, and even for the same pair at different times in the season. Mate guarding may play an important role in accounting for these differences (Weatherhead and McRae 1990, Møller 1991). Brood division may entail fitness costs for the male because the physical separation between male and female as a result of splitting the brood may compromise the extent of mate guarding, and increase the risk of females engaging in extra-pair copulations. For single-brooded species, this should not be a conflict. However, for multi-brooded species, such as the Wood Thrush, the male's decision to attend a portion of an initial brood while the female attends the others may present a trade-off between the advantage of increasing the success of the present brood versus the advantage of assuring paternity for subsequent, same-season broods. Even so, there are reports where the extent of mate guarding was found to be similar between first and subsequent clutches (Møller 1991) or greater for final broods (Weatherhead and McRae 1990, Kopachena and Falls 1993). From our observations of radio-tagged pairs that re-nested, it was evident that male, female, and offspring were moving as a unit. We propose that by keeping all fledglings together and close to subsequent nests, males still may be able to monitor the activities of their mates. During final broods, mate-guarding becomes unnecessary and, as we observed, parents split the brood and moved apart. In agreement with this idea, division of single or final broods, but joint attendance of initial broods has been reported for other species (e.g., Prairie Warbler, *Dendroica discolor,* Nolan 1978; European Robin, *Erithacus rubecula,* Harper 1985; Blackbird, *Turdus merula,* Edwards 1985). Likewise, Ritchison and coworkers (1994) reported no differences in the percentage of extra-pair young in second broods, even when male Northern Cardinals (*Cardinalis cardinalis*) care for fledglings while females initiate another nest. Edinger (1988) proposed that when female Northern Orioles (*Icterus galbula*) stayed close to the nest, their mates may be in visual or auditory contact without close association. He observed that male mate following was significantly more frequent when females ranged more than 120 m from the nest.

Although our sample size is small and our evidence is circumstantial, we suggest that mate-guarding may play a role in parental care for Wood Thrushes. It is evident that more work is necessary to fully understand the costs and benefits for different strategies regarding parental care. For instance, it is necessary to clarify whether or not division of the brood between parents is accompanied by physical separation of the pair. A combination of radio tracking, detailed behavioral observations, and DNA fingerprinting seems to be a promising approach.

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INFLUENCE OF LANDSCAPE AND HABITAT CHARACTERISTICS ON OVENBIRD PAIRING SUCCESS

AMANDA D. RODEWALD[1,2] AND RICHARD H. YAHNER[1]

ABSTRACT.—We investigated the influence of disturbance type (agriculture and silviculture) within forested landscapes, amount of forest cover within 1 km of the site, and local habitat characteristics on the pairing success of Ovenbirds (*Seiurus aurocapillus*) in central Pennsylvania during May and June 1998. Because areas with low pairing success often are inferred to have high nest predation, we also examined whether pairing and nesting success were correlated across sites. We determined the pairing status of 116 male Ovenbirds on 10 sites within contiguous mature forest. Percent of males that were paired on each site ranged from 54–92% (mean = 78%). Pairing success was negatively associated with forest cover within 1 km and positively associated with leaf litter depth. Percent bare ground also was positively correlated with forest cover within 1 km of the site. Estimates of pairing success were unrelated to Ovenbird nesting success at each site (based on 48 nests), which suggests that site-level differences in nest predation or reproductive potential are not necessarily associated with the ability of males to acquire mates. Our data suggest that pairing success of Ovenbirds in forested landscapes is not reduced by the amount of habitat loss within 1 km and is determined by local habitat rather than landscape characteristics. *Received 6 Oct. 1999, accepted 3 Feb. 2000.*

Reduced nesting success of forest birds in fragmented landscapes has been demonstrated by many researchers (Wilcove 1985, Porneluzi et al. 1993, Hoover et al. 1995, Hagan et al. 1996). Recent studies have indicated that pairing success also may be reduced by fragmentation (Gibbs and Faaborg 1990, Villard et al. 1993, Van Horn et al. 1995, Burke and Nol 1998). The Ovenbird (*Seiurus aurocapillus*) is a ground nesting, area sensitive warbler (reviewed by Van Horn and Donovan 1994) that is reported to have lower pairing success in small forested tracts (Gibbs and Faaborg 1990, Villard et al. 1993, Van Horn et al. 1995, Burke and Nol 1998), especially when there is little forest cover within the surrounding landscape (Van Horn et al. 1995). Explanations that have been proposed for the reduced pairing success in small forest fragments include high nest predation, low food availability, avoidance of edges by females, female-biased mortality rates, and large numbers of poor quality or young males (Gibbs and Faaborg 1990, Villard et al. 1993, Van Horn et al. 1995, Burke and Nol 1998). Although empirical evidence is lacking for most of these hypotheses, data show that small forest tracts can have lower arthropod biomass in the leaf litter (Burke and Nol 1998) and lower Ovenbird nesting success (Porneluzi et al. 1993) than large forested areas. However, few studies have directly compared pairing and nesting success estimates on the same sites (but see Porneluzi et al. 1993).

Most research on pairing success of Ovenbirds has been focused on woodlots within fragmented agricultural landscapes (but see Hagan et al. 1996, Sabine et al. 1996), resulting in a limited ability to predict the impacts of disturbances on pairing success in other landscapes. Studies in fragmented silvicultural landscapes have had mixed results regarding associations between landscape characteristics and Ovenbird pairing success (Hagan et al. 1996, Sabine et al. 1996). Investigations in forested landscapes, whether impacted by silvicultural or agricultural disturbances, are still needed to determine thresholds and patterns of habitat alteration that can be tolerated by Ovenbirds.

In this study, we compared the relative influence of landscape versus local habitat characteristics on the ability of male Ovenbirds to acquire mates in contiguous forest habitat within forested landscapes. Our objectives were to (1) determine the influence of disturbance type within the landscape (agriculture and silviculture), amount of forest cover within 1 km from the study site, and local habitat characteristics on pairing success of Ovenbirds in forested landscapes of Pennsylvania

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and (2) test the association between pairing and nesting success among sites.

METHODS

Study sites.—Ten 25-ha sites within contiguous mature forest (approximately 80–110 years old) were selected in the Ridge and Valley physiographic province of central Pennsylvania (40° 40′ N, 77° 55′ W). Boundaries of each site were at least 100 m from a habitat edge. We defined our landscapes as 1 km radius circles (approximately 3.14 km^2 or 314 ha) centered on each study site. Appropriate spatial scales for landscape level studies of most Neotropical migratory birds range in size from several individual territories to a species' distribution over larger regions (Freemark et al. 1995). Because Ovenbird territories range from 0.2–1.8 ha (Van Horn and Donovan 1994), our spatial scale should be sufficiently large to be perceived as a landscape by Ovenbirds. Five sites occurred within forested landscapes disturbed by agriculture (agricultural landscapes) and those disturbed by silviculture (silvicultural landscapes). Agricultural disturbances consisted mainly of row crops with scattered hayfields, whereas silvicultural disturbances were clearcuts (less than 15 years old) with or without scattered residual trees and ranged from 7–38 ha. Sites within the two landscape types had similar amounts of forest cover, ranging from 45–82% within 1 km of the site center. At each site, at least 80% of the non-forest cover within 1 km consisted of only one disturbance type. Other disturbances within the surrounding landscape, such as roads, were similar among sites. All sites had little or no slope, relatively low horizontal heterogeneity (e.g., few internal gaps), and were 250–500 m in elevation. Sites were separated by at least 3 km to maximize independence of the 1 km radius landscapes and still be logistically feasible. Common tree species in the study area include white oak (*Quercus alba*), northern red oak (*Q. rubra*), chestnut oak (*Q. prinus*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), black gum (*Nyssa sylvatica*), black cherry (*Prunus serotina*), and hickory (*Carya* spp.).

Pairing success.—We plotted locations of all territorial males on maps of each site from mid-May to mid-June 1998 at 2–3 day intervals. We assumed that most pairing activity occurred 3–4 weeks following the arrival of Ovenbirds on sites (Gibbs and Faaborg 1990), which was in late April on our sites. From 26 May–10 June 1998, each male was observed for 90 min between 06:00–11:00 to determine pairing status (Gibbs and Faaborg 1990). This protocol has been used in investigations of Ovenbird pairing success from preincubation through nestling stages in Missouri (Gibbs and Faaborg 1990), Québec (Villard et al. 1993), New Brunswick (Sabine et al. 1996), and Ontario (Villard et al. 1993, Burke and Nol 1998). Occasionally, we could not monitor a male continuously during an observation period because of dense vegetation. In these few instances, at least four 30-min observation periods were conducted on the same morning. A male was considered paired if he tolerated a non-singing conspecific within 5 m, courtship fed, fed young, or visited a nest (Gibbs and Faaborg 1990). The observation period ended early if a male was determined to be paired. To verify the effectiveness of the 90-minute observation period, we plotted the number of paired males identified versus total elapsed observation time. At each site, an estimate of pairing success was calculated (% males paired) based on the total number of males observed per site. Over 77% of the paired males were determined to be paired within 30 minutes and over 95% within 60 minutes, suggesting that the 90 minute observation period allowed adequate time to detect evidence of pairing.

Nesting success.—Nest searching efforts for Ovenbirds began on 13 May and continued through mid-July 1998. We marked all the nests we located with numbered flagging placed more than 10 m from the nest. Nests were checked at least every 3–5 days, more often near fledging time. During a nest check, number of eggs (host and cowbird), number of nestlings, activity of parent (if seen), and any disturbance to the nest were noted. For each nest check, the nest was approached by a different route to prevent leaving a scent trail directly to the nest. If a potential nest predator was seen within 50 m of the nest, we postponed checking the nest. Each nest was determined to be successful or failed (success being at least 1 young fledged) based on length of nestling stage, destruction of nest, or detection of the fledglings. Both apparent (% nests successful) and Mayfield estimates of daily nest survival (Mayfield 1961, 1975) were calculated for each site.

Landscape and habitat characteristics.—Two landscape characteristics were examined: disturbance type within a landscape (agricultural and silvicultural) and the amount of forest cover within 1 km of the study sites. Forest cover was determined from classified thematic mapper imagery using ARC/INFO geographic information system software (ERSI 1997). To describe local habitat characteristics, we established three habitat sampling points spaced at 150 m intervals along a transect running approximately through the center of each study site. Because internal vegetative structure and composition of sites were relatively homogeneous based on our visual assessment, we felt that this sampling effort reasonably characterized each site. The following habitat variables were measured at a 0.04 ha circular plot centered on the point (modified from James and Shugart 1970): numbers of trees by species in three dbh (diameter breast height) classes (8–23 cm, 23–38 cm, and >38 cm dbh); standing dead trees in two dbh classes (15–30 cm and >30 cm), numbers of fallen logs (≥7.5 cm in diameter, ≥1.0 m long) and stumps (≥7.5 cm diameter, ≥0.25 m tall; hereafter logs and stumps are collectively referred to as woody debris), soil temperature (° C), soil pH, and soil moisture (%). Soil moisture was not measured during or less than 2–3 days following precipitation. Two 20-m perpendicular transects were established through each sampling point in north-south and east-west directions.

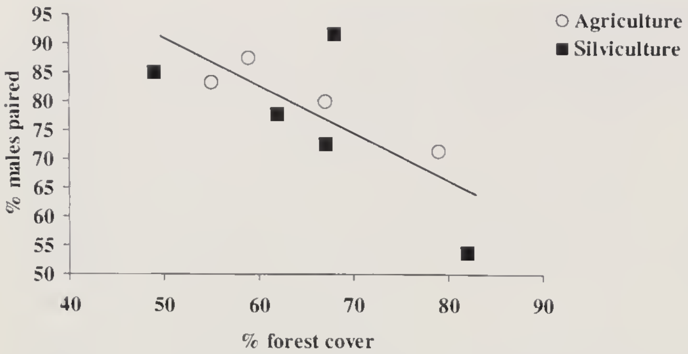

FIG 1. Relationship between Ovenbird pairing success (%) and percent forest cover within 1 km of each study site in forested landscapes disturbed by agriculture or silviculture in central Pennsylvania, 1998. The slope of the regressions is % males paired = 1.28 − 0.01 × (% forest cover).

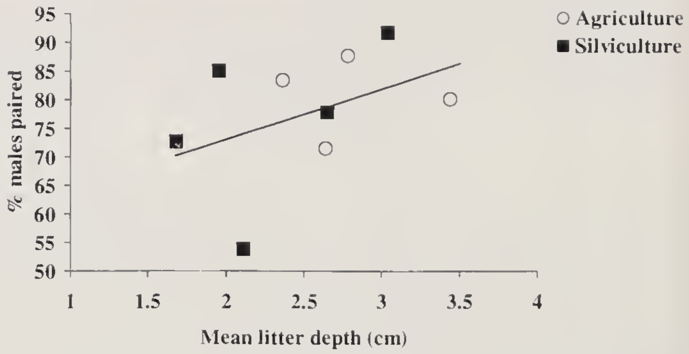

FIG 2. Relationship between Ovenbird pairing success (%) and mean litter depth (cm) at each study site within forested landscapes disturbed by agriculture or silviculture in central Pennsylvania, 1998. The slope of the regression is % males paired = 0.76 + 0.08 × (litter depth).

Percentage canopy cover (using ocular tube sightings) and litter depth (cm) were measured at 2-m intervals along these transects. Within 5 m of each sampling point, numbers of small woody stems (>0.5 m tall, <8.0 cm dbh) in size classes 0–2.5 cm and 2.5–8.0 cm (measured 10 cm above ground) were recorded by species, and percentages of ground cover (<0.5 m in height) by grass, forb, fern, moss, litter, rock, and bare ground were recorded to the nearest 5%. Measurements for each habitat characteristic were averaged over the three points within a site.

Data analysis.—Stepwise-linear regression was used to investigate the relationship between site pairing success and landscape and local habitat characteristics (Sokal and Rohlf 1995). Several highly correlated ($r > 0.7$, $n = 9$, $P < 0.01$) or collinear variables were either dropped or combined into the following new variables: total number of trees (≥8.0 cm dbh), total number of small woody stems (<8.0 cm dbh), percentage herbaceous ground cover (grass, fern, forb, and moss), and percentage nonvegetated ground cover (soil, leaf litter, and rock). Leaf litter depth, numbers of snags, amount of woody debris, soil pH, soil temperature, landscape type, and percent forest within 1.0 km also were included in our regression analysis. At each step in the analysis, a F-statistic was calculated for each independent variable in the model. Only full models with $P < 0.05$ were considered significant. Individual variables having a significance level of $P < 0.20$ were allowed to enter the model initially but later were removed if $P > 0.10$ after the inclusion of other variables. Because we had low confidence in estimating both pairing and nesting success at one site because of too few observations during the sampling period, it was excluded from analyses. Relationships between pairing and nesting success were examined using Pearson correlation analysis. Data and residuals were checked for normality, homogeneous variance, the presence of outliers and/or influential observations. All statistical analyses were conducted using SAS for Windows software, version 4.0 (SAS Institute, Inc. 1990).

RESULTS

Pairing status was determined for 116 male Ovenbirds (7–20 per site), success ranged from 54–92% of the males per site. Mean estimated pairing success was similar between contiguous forest sites within agricultural and silvicultural landscapes [81% ± 3.41 (SE) vs 76% ± 6.45, $n = 9$]. Pairing success was negatively associated with percent forest cover within 1 km (partial $R^2 = 0.52$, $F_{1,7} = 7.63$, $P = 0.03$; Fig. 1) and positively associated with leaf litter depth (partial $R^2 = 0.24$, $F_{1,7} = 5.82$, $P = 0.05$; Fig. 2) on a site (Full model: $R^2 = 0.76$, $F_{2,6} = 9.35$, $P = 0.01$). No other variables met the significance level required to be included in the model. This was also true for a regression model that included the category of small woody stems (<2.5 cm diameter) rather than the combined woody stem variable (<8.0 cm dbh). Percent forest cover within 1 km was positively correlated with percent bare ground at a site ($r = 0.66$, $n = 9$, $P = 0.04$).

Forty-eight Ovenbird nests were located (mean of 5.3 nests per site). Nesting success ranged from 40–67% (51.78 ± 3.56), and Mayfield daily survival estimates ranged from 84–98% (92.89 ± 1.41). However, pairing success on a site was unrelated to either apparent nesting success ($r = -0.49$, $n = 9$, $P > 0.05$) or Mayfield daily survival estimates ($r = 0.21$, $n = 9$, $P > 0.05$).

DISCUSSION

In contrast to previous studies that report reduced Ovenbird pairing success with increased fragmentation in highly altered landscapes (Gibbs and Faaborg 1990, Villard et al. 1993, Van Horn et al. 1995, Hagan et al. 1996, Burke and Nol 1998), we found the opposite pattern. We suspect that this difference is due to the fact that all of our landscapes were heavily forested relative to those other areas and, thus, probably were not disturbed enough to compromise pairing success. In forested landscapes in New Brunswick, Sabine and coworkers (1996) also failed to detect a negative association between Ovenbird pairing success and forest area. Even though landscape characteristics, such as type of disturbance and amount of forest cover, are known to influence bird communities (Andrén 1992, Friesen et al. 1995, Bayne and Hobson 1997, Donovan et al. 1997), the significant association we detected between forest cover and bare ground on sites raises the possibility that the ability of males to acquire mates was a function of characteristics at the local scale only.

We suggest that observed patterns of pairing success are best explained by local differences in habitat characteristics among sites. Leaf litter depth and bare ground, in particular, should be important because Ovenbirds forage by gathering invertebrates from leaf litter on the forest floor (Holmes and Robinson 1988, Van Horn and Donovan 1994). Indeed, previous workers showed that litter depth may be a cue used by females to select nest sites (Van Horn and Donovan 1994), and litter depth is deeper in occupied Ovenbird territories versus random locations (Burke and Nol 1998) and territories of paired versus unpaired males (Van Horn et al. 1995). Ovenbirds may use structural habitat cues, such as litter depth, to assess habitat quality and prey abundance (Smith and Shugart 1987). Leaf litter depth is thought to indicate invertebrate biomass, which was greater in occupied Ovenbird territories than in random locations in Ontario (Smith and Shugart 1987, Burke and Nol 1998; but see Sabine et al. 1996). In addition, Burke and Nol (1998) reported lower pairing success in fragments with significantly more bare ground and less developed seedling and shrub layers than in large forest tracts. Thus, we believe that the negative relationship that we observed between forest cover and pairing success may represent a statistical artifact rather than an ecological relationship.

A link between pairing and nesting success has been proposed several times (Gibbs and Faaborg 1990, Villard et al. 1993) and is thought to contribute to low pairing success on small forest fragments. Because small forest fragments generally have higher rates of nest predation than large forest tracts, researchers have suggested that a male-biased sex ratio may result if females avoided small fragments or were killed during incubation or brooding. Presumably, a similar situation might occur in forested landscapes that differed in nesting success. Despite variation in both Ovenbird pairing and nesting success among our study sites, pairing and nesting success were unrelated. This suggests that site-level differences in nesting success were not responsible for variation in the ability of males to acquire mates. However, associations between pairing and nesting success may be temporally offset, where low observed pairing success may reflect prior, not current, elevated predation rates.

Our data suggest that in landscapes with extensive and contiguous forest, pairing success of Ovenbirds is not reduced by limited amounts of habitat loss in the surrounding landscape and is a function of local habitat rather than landscape characteristics. Because we detected no correlation between pairing and nesting success for Ovenbirds across sites, differences in nesting success failed to explain the observed variation in Ovenbird pairing success. Although our sample sizes of both sites and nests were relatively small and limited to only one field season, the absence of a clear relationship between pairing and nesting success leads us to caution against the use of pairing success as an index to reproductive potential. Previous studies of forest birds in highly modified landscapes have given us considerable insight into the impacts of landscape alteration on breeding bird pairing and nesting success. Examination of these phenomena in relatively forested landscapes is essential to understand patterns and thresholds of habitat alteration that can be tolerated by sensitive forest birds.

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BREEDING SEASON DEMOGRAPHY AND MOVEMENTS OF EASTERN TOWHEES AT THE SAVANNAH RIVER SITE, SOUTH CAROLINA

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ABSTRACT.—The Eastern Towhee (*Pipilo erythrophthalmus*) has undergone population declines across much of its range, especially in New England. Despite being a widespread and, at one time, a common species, relatively little is known about its natural history, ecology, or demographics. We conducted baseline research on Eastern Towhees at the Savannah River Site, South Carolina, in 1995 and 1996 to estimate breeding season survival rates, nest success rates, breeding densities, and daily movements. We also were interested in whether towhees had differences in survival and movement rates between young and mature managed pine stands. We found that survival rates during the breeding season of radio-marked towhees did not vary by sex or stand type. Daily nest success rates were very low [0.629 ± 0.088 (SE)] as a result of high predation levels. Abundance estimates adjusted for sampling effort differed between years. In 1995, the abundance estimate was significantly lower in mature stands (7.1 ± 0.47) than in young stands (9.6 ± 0.60) while in 1996, there was no different between mature stands (26.2 ± 5.67) and young stands (16.5 ± 3.39). Average daily movements by radio-marked towhees did not vary by sex or stand type. Movements among adjacent stands were common, and sometimes great distances. *Received 22 Sept. 1999, accepted 22 Dec. 1999.*

Eastern Towhees (*Pipilo erythrophthalmus*) were once a widespread and common breeding bird throughout Eastern North America (Greenlaw 1996). Since at least 1966, Eastern Towhee populations have declined sharply throughout most of the species' range, especially in New England (Hagan 1993, Sauer et al. 1997). The principal causes for these declines are thought to be habitat loss, habitat alteration, and increased mortality rates, especially of nesting females (Hagan 1993, Greenlaw 1996). Habitat alteration is mostly due to agriculture and forest management practices that reduce ground and mid-story cover.

Only one estimate of annual survival rate has been reported for Eastern Towhees (DeSante et al. 1996) but none during the breeding season. The propensity of towhees to forage and nest on or near the ground probably exposes them to high rates of reptilian and mammalian predation (Brawn et al. 1995). This exposure to ground dwelling predators may in part underscore the need to estimate sex-specific and breeding period survival rates (Greenlaw 1996). Baseline reproductive data are available on age at first breeding, clutch size, length of breeding season, and numbers of broods per season, but information on nest success rates is minimal (Greenlaw 1996). More importantly, conservation efforts require documentation of variation in reproductive effort across seasons, years, ages, and habitat types (Hagan 1993).

Censuses of Eastern Towhees have been conducted across various habitats based on territory mapping procedures (Greenlaw 1996). These density estimates range widely, no doubt in part because of differences in techniques used. Eastern Towhees are surveyed well by the Breeding Bird Survey (Sauer et al. 1997). Range maps suggest recent differences in densities across the range of the towhee, but no range retractions are evident (Greenlaw 1996).

Our objectives were to estimate Eastern Towhee breeding season survival rates, nest success rates, densities, and daily movement distances.

STUDY AREA AND METHODS

We studied Eastern Towhees at the Savannah River Site (SRS), a National Environmental Research Park, in western South Carolina along the Savannah River in Aiken, Barnwell and Allendale counties. Savannah

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River Site is a 770 km^2 U.S. Department of Energy facility that lies in the Upper Coastal Plain physiographic province. At the site, towhees inhabited understory grass and shrublands in mature loblolly pine (*Pinus taeda*) and longleaf pine (*P. palustris*) stands, and in replanted clearcut stands (Krementz and Christie 1999). Replanted stands were occupied by towhees until the canopy closed and the mid-story and ground cover declined after about 10–15 years. Mature pine stands were managed with periodic thinning and burning (cool and warm season) on a 3–5 yr rotation. All mature stands we monitored were burned within the previous 3 years.

In 1995, we monitored birds in 8 young longleaf pine stands and 8 mature longleaf pine stands. Young stands were 2–5 years old and from 3–26 ha. Mature stands were 32–97 years old (median = 53) and from 6–59 ha. In 1996, we used 12 young longleaf pine stands and 4 mature longleaf pine stands. Young stands were 3–6 years old and from 3–57 ha. Mature stands were 38–98 years-old (median = 57) and from 10–53 ha.

We captured towhees by placing 20 12-m (30-mm) mist nets in a 5 × 5 grid (1995, 4 ha) or a 5 × 4 grid (1996, 3 ha) with nets 50 m apart. Birds were captured during 3 sampling rounds in 1995 (25 April–24 May, 25 May–23 June, and 26 June–21 July) and 1996 (1 May–30 May, 1–28 June, and 1–30 July). We sampled all stands once per round.

Each day, beginning 30 min before sunrise, we opened mist nets for 4 h and closed them earlier only when precipitation exceeded 0.5 cm/h or temperatures exceeded 30° C. We checked nets at 30–45-min intervals, more often when weather conditions threatened the health of netted birds. For each captured bird, we recorded age and sex (Pyle et al. 1987), and banded each bird with a USGS-Biological Resources Division leg band. We also treated recaptures at different stands within the year as new individuals because our telemetry observations indicated that movement among monitored stands was low, and we had no comparable checks for unmarked birds moving among stands.

Beginning on 7 May 1996, we attached radio transmitters to 20 towhees (9 M, 11 F) using a thigh harness (Rappole and Tipton 1991, Powell et al. 1998). The radio with harness weighed 1.3–1.4 grams, or about 3% of body mass. We monitored each bird's status (dead, alive, censored) and location (UTM ± 20 m) daily until either radio failure or the end of the study period (18 July). Birds alive on 18 July were considered to have survived the breeding season. We did not begin tracking until 13 May after which time we estimated a 10 week survival rate.

At the end of each week's monitoring, every radio-tagged bird was categorized as survived, censored, or dead. Mortality was assigned to individuals when the recovered radio or radio harness was disfigured or the carcass was found. Survival was assigned if the bird was seen alive or if the radio signal was lost shortly after an indication of battery failure (e.g., variable pulse rate). An individual was censored if the radio failed prematurely without warning or if the harness and radio were found under conditions for which neither mortality nor survival of the individual could be determined. We identified predators by examining physical evidence at the recovery site.

Cohorts of radio-marked towhees were used to estimate weekly survival probabilities using the program SURVIV (White 1983). We tested for both sex-specific and stand type specific (young/mature pine stand) effects on survival rates by comparing general (specific survival rate estimates) and constrained (combined estimates of survival rate) models using Aikike's Information Criteria (AIC; Burnham and Anderson 1998). If the AIC values for competing models were less than 2 units different, we relied on the Likelihood Ratio Test to determine which model the data fit better (Burnham and Anderson 1998). Finally, we estimated an overall weekly survival rate combining sexes and stand types.

In 1996, nests were found by monitoring radio-tagged females. We used at least 5 consecutive daily readings at the same location as evidence of nesting. We began looking for nests of radio-tagged females on 16 May. Occasionally nests were located by flushing unmarked towhees from a nest. Once located, nests were monitored every 2–4 days until the nest failed or nestlings fledged. Date, number of eggs or nestlings, and number of Brown-headed Cowbird (*Molothrus ater*) eggs were noted at each nest.

Nests that fledged at least one young were considered successful. Nest survival rates were estimated using a modified Mayfield (1975) approach incorporating the exact number of days between nest checks for increased survival rate precision (Bart and Robson 1982).

We estimated abundance for the mist net grids in each stand type. If a bird was captured once during any 2-day monthly capture period, it was recorded as present, otherwise it was categorized as absent. Only capture histories for adults were used for analyses. Abundance was estimated using the program MARK (White 1999). In 1996, these abundance estimates were not comparable between stand types because we sampled different numbers of stands per stand type (12 young, 4 mature). To correct for the differential sampling effort, we estimated an adjusted relative abundance ($\hat{N}_i'$) by dividing the abundance ($\hat{N}_i$) of stand type i (where i = mature or young stands) by the number of stands sampled (n_i). Variance for this estimate was derived as:

$$v(\hat{N}_i') = v(\hat{N}_i) \times \left(\frac{1}{n_i}\right)^2$$

where n = the number of stands sampled. Relative abundance ($\hat{N}_i'$) between stand types was compared using a 95% confidence interval (CI).

We measured daily distances moved based on consecutive daily radio tracking locations. Because Krementz and Pendleton (1994) found that differences in daily distances moved among individual American

TABLE 1. Sample sizes, cumulative number of weeks tracked, numbers survived, censored, and died of radio-marked Eastern Towhees by stand type and sex at Savannah River Site, South Carolina.

Stand type Sex	*n*	Weeks tracked	Survived	Censored	Died
Mature					
Male	3	16	1	2	0
Female	5	30	3	1	1[a]
Young					
Male	6	46	3	3	0
Female	6	43	4	2	0

[a] Source of mortality was an unidentified mammal.

Woodcock (*Scolopax minor*) often overwhelmed the effects of sex and age on movements, we used the average distance moved per day per individual as a response variable. We excluded all individuals with less than 10 daily movements to reduce the effects of individual birds with small sample sizes. We investigated whether sex, stand type, or the interaction of sex and stand type explained variation in daily movements using a linear model (PROC GLM; SAS version 6.02 on an IBM PC; SAS Instit. 1990).

All means presented are ±1 SE.

RESULTS

We radio-tagged 20 towhees between 7 May, and 13 June 1996. Half of the sample was marked by 16 May and only one death was documented (Table 1). More males were censored (4 of 9) than females (3 of 11). Censoring occurred throughout the study period and was not related to any weather events.

We found no differences in survival rates between sexes or stand types (Table 2). Therefore we estimated a combined overall weekly survival rate (Table 2).

Nests were located in grape (*Vitis* spp., 3), sparkleberry (*Vaccinium arboreum,* 2), oaks (*Quercus* spp., 2), common persimmon (*Diospyros virginiana,* 1), wax-myrtle (*Myrica cerifera,* 1), and broomsedge (*Andropogon virginicus,* 1). All marked females either had developed brood patches when captured or were observed being courted, nest-building, feeding young, or all of the above. While under observation, 5 females exhibited nesting behavior once, 2 females twice, and 3 females three times. We located 1 nest for one

TABLE 2. Weekly survival rate (±1 SE) estimates and test statistics by sex, stand type, and pooled for radio-marked adult Eastern Towhees during the breeding season at Savannah River Site, South Carolina

Factor				Likelihood Ratio Test		
	ϕ	SE	Akaike's Information Criteria	χ^2	*n*	*P*
Pine stand age						
Young	1.000	0.1060				
Mature	0.979	0.0206	10.502[a]			
Pooled stand data	0.993	0.0073	10.613[b]	2.11[c]	1	0.15
Sex						
Male	1.000	0.1259				
Female	0.986	0.0134	10.436[a]			
Pooled sex data	0.993	0.0073	9.674[b]	1.24[c]	1	0.26
Pooled survival rate	0.993	0.0069				

[a] General model test fit statistic (e.g., whether habitat specific survival rates were necessary to model the data).
[b] Constrained model test fit statistic (e.g., whether a combined habitat survival rate was sufficient to model the data).
[c] Likelihood ratio test for fit between models (e.g., analogous to the constrained AIC test statistic).

female, 2 nests for two females and 3 nests for one female. Overall, we monitored 10 nests (9 during egg/nestling period, 1 during the nestling period). Only 3 egg clutches were found. Two nests were parasitized by Brown-headed Cowbirds with 1 cowbird egg per nest. The shortest time between the young fledging from one nest and the start of nest construction on the next nest for an individual female was one week. Of 10 nests monitored, only 1 nest fledged young. On separate occasions, three marked males were observed with fledglings. All other nests were destroyed by unknown predators. Across stand types (7 young and 3 mature), the daily survival rate during egg stage was 0.661 (±0.0875). For the egg and nestling periods combined, the estimated daily survival rate was 0.619 (±0.0811).

We captured 51 towhees (33 in young stands and 18 in mature stands) in 1995 with 11 recaptured at least once. The adjusted abundance estimate ($\hat{N}_i'$) in the 4 ha plots was 9.6 (±0.60) for young stands and 7.1 (±0.47) for mature stands; respective densities were 2.4 and 1.8 birds per ha. We estimated that more towhees were found in young pine stands than in mature stands because the 95% CI's for ($\hat{N}_i'$) did not overlap (young: 8.5–10.8; mature: 6.2–8.0). We captured 60 towhees (49 in young stands and 11 in mature stands) in 1996 with 7 recaptured at least once. The adjusted abundance estimate ($\hat{N}_i'$) in the 3 ha plots was 16.5 (±3.39) for young stands, and 26.2 (±5.67) for mature stands; respective densities were 5.5 and 8.7 birds per ha. There was no difference in the relative abundance of towhees in mature and young pine stands as the 95% CI's for ($\hat{N}_i'$) overlapped (young: 9.9–23.2, mature: 15.1–37.3).

Seventeen individuals met our minimum requirements for analysis of daily movements. Except for the incubation period when females were always on their nests, both sexes typically moved over the entire stand where they were captured. Only 2 birds, both females, remained in the stands where they were captured. The remaining 15 birds moved among adjacent stands. Stand types used included pine stands from just replanted to those over 75 yr old. Towhees marked in young pine stands used either middle aged (ca 20–35 yr) or mature stands, whereas towhees marked in mature stands also used middle-aged stands. No towhees moved from either a young or mature stand to a young stand. These movements were not permanent movements, but represented daily activities. Daily movement averaged 99 m/day (±10.46), with daily movements ranging from 39–173 m/day. The maximum distance moved per marked bird over each individual's sampling period averaged 464 m (±64.18), with maximum distances ranging from 110–1250 m. We found no effect of sex ($F_{1,16} = 0.99$, $P > 0.05$), stand type ($F_{1,16} = 0.12$, $P > 0.05$) or interaction between sex and stand type ($F_{1,16} = 0.74$, $P > 0.05$) on daily distances moved.

DISCUSSION

Weekly breeding season survival rates of towhees in 1996 (0.993 ± 0.0069) did not vary by habitat type. Stober and Krementz (unpubl. data) did not find any differences between breeding season survival rates for Bachman's Sparrows (*Aimophila aestivalis*), another scrub species that uses young and mature longleaf pine stands at our study site. The absence of any difference in survival rates for either of these scrub birds between such seemingly different seral stages is surprising. One interpretation of this similarity in habitat-specific survival rates is that these scrub birds rely only on the mid-story and ground cover for their needs, that is, they do not 'see' the forest overhead.

Our estimates on nest success during the egg stage and for the entire nest stage were quite low compared to most passerines (Martin and Li 1992), but may be representative of Eastern Towhees from the Northeast (J. S. Greenlaw, pers. comm.). We suspect that nest success during 1996 was low based on the findings of Stober and Krementz (unpubl. data) who worked at the same study site on nesting success of Bachman's Sparrow (*Aimophila aestivalis*). Bachman's Sparrows are an appropriate bird to compare with towhees because they use similar microhabitats within the pine sere. The daily nest survival rate in Bachman's Sparrows in 1995 was 0.952 (±0.013, $n = 26$), while in 1996, it was 0.889 (±0.027, $n = 15$). Daily nest survival was significantly lower in 1996 than in 1995, when only 1 of 15 sparrow nests fledged one individual (Stober and Krementz, unpubl. data).

Caine and Marion (1991) reported towhee densities in middle aged (20–25 yr-old) pine plantations in north-central Florida from 2.1–4.2 pairs/km^2 (0.02–0.04 pairs/ha). From their descriptions, the stands of Caine and Marion (1991) most closely resembled our mature stands. Our density estimates of 2.4–8.7 birds/ha far exceeded those of Caine and Marion (1991). This again supports Greenlaw's hypothesis that towhee densities vary within habitat types.

Our sampling methods were not designed to monitor within day movements but instead were set up to monitor movements within the breeding season. Of those birds not censored (13 of 20), among-day movements during the breeding season were short (ca 100 m/day). In most cases, all birds had an area of central activity as was found by Greenlaw (1969). In addition, we found that excursions away from the central activity area were common, sometimes long (1250 m), and crossed through different aged pine stands. Middle aged pine stands were the usual target of these movements. Why towhees did not move to young stands is perplexing.

Our findings indicate that towhee breeding season survival rates are high, but that nest success rates are low. These low nest success rates, if occurring elsewhere, may be contributing to the observed population declines. Towhees appear flexible in their habitat requirements as long as there is a well developed mid-story and ground cover. Therefore, we recommend that land managers concerned with scrub-successional species like the towhee take appropriate management actions (e.g., selective harvests and prescribed burning) to produce optimal habitat.

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Announcement

The Lincoln Park Zoo Africa/Asia Fund supports field research in conservation biology throughout Africa, Asia, and the Pacific. The fund emphasizes support of graduate students and other young researchers, particularly those from Africa and Asia. The fund, launched in 1997, supports between 5 and 15 projects each year. Awards are seldom greater than US$7500, and most awards fall in the range of $3000–$6000. Initial support is for up to 12 months from the date of award. Maximum duration of support is two years. Deadline for receipt of Africa/Asia proposals is 1 September. For additional information and application procedures go to www.lpzoo.com/conservation, email conservation@lpzoo.org, or write to: LINCOLN PARK ZOO AFRICA/ASIA FUND, Department of Conservation and Science, Lincoln Park Zoo, Chicago, IL 60614.

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USE OF SUCCESSIONAL HABITAT AND FRUIT RESOURCES BY SONGBIRDS DURING AUTUMN MIGRATION IN CENTRAL NEW JERSEY

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ABSTRACT.—We evaluated the effects of plant succession on habitat use and fruit resource availability for autumn migratory and resident songbirds in 43 ha of abandoned farm fields in central New Jersey. Using fixed net sites, standardized effort, and simultaneous sampling across habitat types, we mist-netted birds to compare habitat use and found that (1) use of three shrub-tree invasion interfaces declined as fruit-bearing shrubs were overgrown by trees, while use of three open shrublands changed little over the same period; (2) use of two pairs of contrasting successional habitats, shrubland and young woodland, was higher in the shrubland with abundant, highly nutritional fruits than in young woodland with sparse fruit; and (3) use of three shrublands at similar successional stages but with different fruit availability differed by bird taxonomic family and migratory strategy. Data on species composition and relative abundance of fruit-bearing shrubs and fruit consumption by birds (assessed by regurgitated and defecated matter) were used to elucidate avian patterns of habitat use. The relative abundance of fruit-bearing species may be more important than habitat structure in determining habitat use by birds. Shrubland dominated by panicled dogwood (*Cornus racemosa*) was favored over shrubland dominated by red cedar (*Juniperus virginianum*) or multiflora rose (*Rosa multiflora*). Favored vines were Japanese honeysuckle (*Lonicera japonica*), Virginia creeper (*Parthenocissus quinquefolia*), poison ivy (*Toxicodendron radicans*), and grape (*Vitis* spp.). *Received 26 April 1999, accepted 29 Dec. 1999.*

Recently researchers on migratory songbird populations have emphasized the need for better knowledge of habitat and resource requirements during spring and autumn migration (Keast and Morton 1980, Hagan and Johnston 1992, Moore et al. 1993). Nearctic-Neotropical migrants require stopover habitats to amass stored fat to fuel their extended flights to wintering grounds in the West Indies and Central and South America. However, few researchers have explicitly examined food abundance or resource availability during migration to determine the most important stopover habitats for migratory birds, where such habitats occur, or how habitat distribution and abundance are changing as a result of development and land conversion (Moore and Simons 1992). Fewer researchers have examined habitat use in autumn migration (see Winker et al. 1992, Weisbrod et al. 1993, Parrish 1997, Yong et al. 1998). Autumn migrations of songbirds have been monitored for decades (see Baird et al. 1957, Eastern Bird Banding Association News 1969–1975, North American Bird Bander 1976–1999); however, detailed habitat data are not reported with bird capture data.

New Jersey straddles two important migratory flyways, the Atlantic Coast in the east and the Delaware River Valley in the west. The objective of this study in central New Jersey was to elucidate three questions concerning autumn migrant songbirds: which successional habitats do autumn migrants use most frequently, what are the effects of plant succession on use of these habitats, and what is the relationship between fruit availability and habitat use?

STUDY AREA AND METHODS

Study area.—The study site (40° 25′ N, 74° 46′ W) was located at 134 m elevation in the Sourland Mountains Piedmont physiographic province in Hopewell Township, Mercer Co., west-central New Jersey. The area consisted of 7 abandoned fields totaling approximately 43 ha: Fields 1–4 (each ca 6.5 ha) and Field 10 (1.8 ha). Fields 1–4 were last cultivated in 1959 but the center of Field 2 was plowed parallel to the net lane in 1978. Field 10 was last mowed in 1970. The fields are bordered by country roads, a woodlot, 11 houselots, and a forest tract of approximately 300 ha (Fig. 1, see Suthers 1988 for details).

Yearly vegetation surveys were initiated in 1977 (Suthers 1988). The habitat of each field was characterized by layers of vegetation (herb, shrub and tree), height, and percent of cover by each layer (James and

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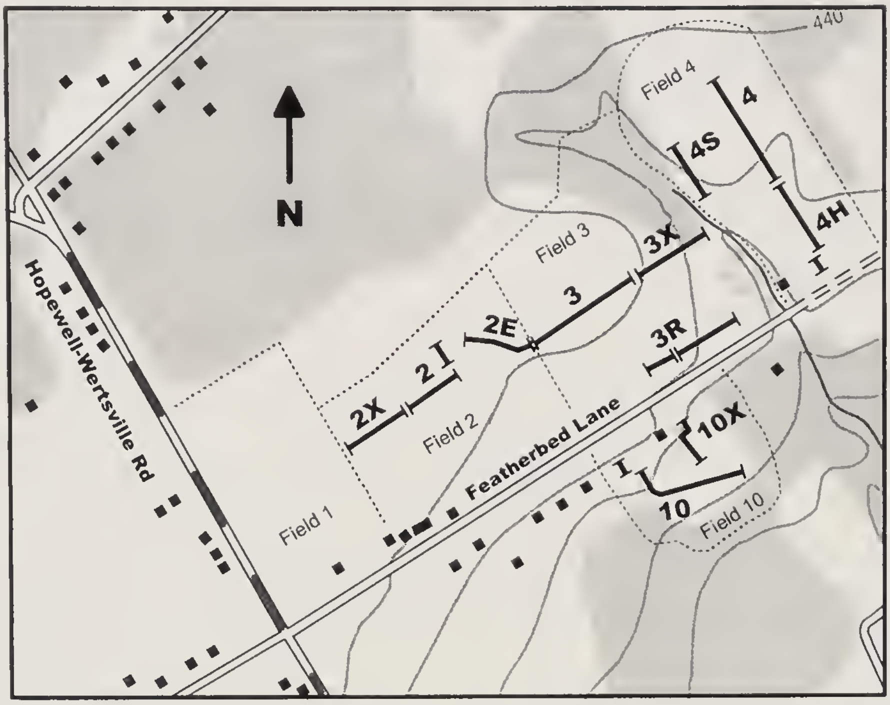

FIG. 1. Map of old fields in the study area showing fixed locations of mist nets superimposed on the 1954 USGS Topographic Map, Hopewell Quadrangle. The gray represents the extent of forest before the successional changes described in Suthers (1988) and in this paper. Contour intervals are 6.1 m (20 feet), the highest being 134 m (440 feet). Darkened squares are homes and barns. In comparisons of bird captures during long term successional changes, Lanes 2X and 10 were open shrublands, Lane 2 was an intermediate shrubland, Lane 2E was a shrub-tree interface, Lanes 10X and 3 were shrubland-tree invasions. In comparisons during short term contrasting stages, Lanes, 3, 3X, and northern portions of Lanes 4 and 4S were young woodlands and Lane 2, and southern portions of Lanes 4 and 4S were wooded shrublands. In comparisons of same stage, unequal fruit resources, Lanes 2, 3R and 10 were wooded shrublands, dominated by panicled dogwood, red cedar and multiflora rose/vines, respectively.

Shugart 1970, DeSante and coworkers 1993). Herbs were defined as grasses, sedges, rushes, forbs, and woody seedlings less than 0.5 m high, shrubs (including sapling trees) as woody plants 0.5–5 m tall, subcanopy as young trees and shrubs 5–10 m tall, and canopy as trees 10 m or greater.

Habitats were designated according to the successional stages surrounding the fixed net lanes at the time of the various comparisons. Open shrublands had about 30% cover up to 1 m high dominated by panicled dogwood (*Cornus racemosa*) or multiflora rose (*Rosa multiflora*), and 70% cover by grasses and forbs dominated by goldenrods (*Solidago* spp., *Euthania* spp.). Intermediate shrublands had about 50% cover over 1 m high that included a few scattered deciduous and red cedar (*Juniperus vrginianum*) saplings. Dense shrublands had about 85% cover up to 2.6 m high that included scattered saplings and vines at shrub height. Wooded shrublands had up to 75% shrub cover over 2 m high, dominated by panicled dogwood in Lane 2, red cedar in Lane 3R, and multiflora rose/vines in Lane 10, and 30–50% mixed deciduous tree cover up to 7–9 m high, that included various vine species that climbed up the trunks. Shrub-tree interface had 50% shrub cover of panicled dogwood 2 m high that interfaced with a dense invasion of 3 m high red maple (*Acer rubrum*) saplings and mixed hardwood seedlings. Tree invasions had 90% cover of mixed deciduous trees less than 9 m high that either preempted or shaded out shrubs and forbs. Young woodlands had 19% canopy cover up to 12 m high, 60% subcanopy cover up to 8 m high, 1–20% dwindling shade-intolerant shrub cover, and a sparse forb cover.

In autumn 1991–1993, species and abundance of fruit-bearing shrubs within 2 m of the net lanes were recorded. In September–October 1995–1997 fruit abundance and rate of disappearance was assessed on bird sampling days. In each lane fruits were counted on marked branches of 10 plants each of various species. Panicled dogwood ripened in mid-August and was available until mid-October. Autumn-olive (*Elaeagnus umbellata*), Virginia creeper (*Parthenocissus quinquefolia*), and frost grape (*Vitis vulpina*) fruits ripened in September and were consumed by late October. Multiflora rose ripened in late September, red cedar, poison ivy (*Toxicodendron radicans*), and Japanese honeysuckle (*Lonicera japonica*), ripened in October, and the fruits persisted into winter.

Bird surveys.—Bird abundance data were collected by mist-netting simultaneously in two or three fields of contrasting or similar vegetative structure in September–November, 1979–1997. The fields were transected with mist nets (12 m, 4 shelf, 30-mm mesh) set end to end in fixed sites, primarily oriented northeast-southwest (Fig. 1). There were 15 nets in Field 2 (Lanes 2, 2E, 2X), 26 nets in Field 3 (Lanes 3, 3X,

TABLE 1. Comparisons of successional habitat use by fall migratory songbirds in September and October in central New Jersey piedmont.

Habitat	Lane	No. nets	Years operated	Days	Net hours	Birds
Long term successional changes						
Shrub-tree interface	2E	3	1979–1993 (no 1981, 1987)	40	667	286
Open shrubland	2X	4	1979–1983, 1992–1993, all simultaneously[a]	(16)[b]	803	554
Shrubland-tree invasion	10X	5	1982–1985	12	300	93
Open shrubland	10	5	Simultaneously	(12)	300	267
Shrubland-tree invasion	3	7	1984–1993 (not 1987, 1991)	(38)	1330	285
Intermediate shrubland	2	6	1979–1980, 1982–1983, then 1988–1993 simultaneously	53	1539	928
Short term contrasting stages						
Wooded shrubland	2 + 2X	7, 12	1989; 1992–1993	21	1110	582
Young woodland	3 + 3X	7, 12	Simultaneously	(21)	1110	149
Wooded shrubland	4 + 4S	4 + 3	1994	8	280	97
Young woodland	4 + 4S	4 + 3	Simultaneously	(8)	280	11
Fruit resources in three shrublands						
Dogwood dominated	2	7	1989–1991, 1995–1997	36	1260	568
Red cedar dominated	3R	7	Simultaneously	(36)	1260	428
Rose and vine dominated	10	7	Simultaneously	(36)	1260	579
				170	11,499	4827

[a] Nets were operated during the same years, days, and hours as the respective habitat being compared.

[b] Parentheses indicate number of days operated simultaneously with the habitat being compared.

3R), 23 nets in Field 4 (Lanes 4, 4H, 4S), and 15 nets in Field 10 (Lanes 10, 10X). Nets (20–32/day) were hung at daybreak one morning a week in the designated sites for comparison (Table 1).

Captured birds were collected every 30 min and placed in ventilated, individual compartments in holding boxes prior to processing. The net site of each capture was noted. Birds were processed within 30 min. They were identified and banded with U.S. Geological Service serially numbered bands. Data were taken on measurements, age, sex, weight, amount of fat in the furculum on a scale of 0–3 (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1977), and molt.

Because this was a study of habitat use by migrants and not temporal patterns of occurance during migration, capture data from weekly samples over 19 years were considered to be representative of habitat use patterns and smoothed from effects of yearly variations in vegetative growing seasons and weather. To document habitat use during successional changes over many years (long term), birds were captured in a shrub-tree interface and two shrubland-tree invasions as they succeeded to woodlands and in three slowly changing shrublands for comparison (Table 1). To determine whether birds preferred shrublands or woodlands, data were taken over a few years (short term) between two pairs of contrasting successional stages, wooded shrublands and young woodlands. To determine if there were shrubland preferences, habitat use was compared among three shrublands at similar successional stages but with different dominating fruit resources: panicled dogwood, red cedar, or multiflora rose and vines.

There may have been a mist net bias in the wooded shrubland–young woodland comparisons because vegetation was shorter in the wooded shrublands and could have resulted in more effective sampling. However, the difference in height was small (1 m) and bias alone (Remsen and Good 1996) would not explain the large differences in capture rates. Birds were rarely observed foraging above the mist nets in the young woodlands, especially after hard frost in early to mid-October. Consequently, it was reasonable to assume that differences in captures during simultaneous sampling reflected abundance, that is, use of the habitat, rather than capture rate biases. Although there are inherent biases in mist net sampling, it is a useful and acceptable technique when done with field observations (Karr 1979, 1981; Remsen and Good 1996).

Fruit consumption survey.—In 1981–1982 and 1995–1997, after removing each bird from its compartment, any regurgitated or fecal matter was removed and all seeds found were identified by comparison with a reference collection gathered from the same locations. Field observations of fruit consumption also were recorded. Blake and Loiselle (1992) recommended fecal sampling because it was less biased than direct observation.

Data analysis.—The few (0.9%) birds recaptured from the previous season's annual breeding studies were considered to be using the habitat as autumn birds, and were included in our analyses. November captures were considered to be migrants arriving to overwinter and were excluded from the analyses.

In the long term comparisons of successional changes, days of operation and net numbers in a habitat were not exactly matched with those of the shrubland habitat (Table 1). Therefore, data were standardized by using bird captures per 100 net hours (b/100 nh). Net hours were the number of nets × hours in operation (Karr 1981). Linear regression was used to examine the number of birds/nh for each habitat with itself each year. In the short term contrasting stages comparisons, and in the fruit resources comparisons the data were used from matched effort within and between years; therefore, the actual numbers of birds captured per day were used as the unit of analysis. Short term data over the years were pooled within each habitat type because they were similar based on linear regressions or Mann-Whitney *U*-test, all with $P > 0.05$. The pooling of short term years increased the samples and also assured that the bird catches were not peculiar to any particlar year of sampling. Short term use of the wooded shrublands and young woodlands were tested by the Mann-Whitney *U*-test. Pairs of categories, namely habitat use by family and by migratory strategy (Leck 1972, Robbins et al. 1989, Rappole et al. 1983), were tested by χ^2 with Yate's Correction. Differential use of shrublands with unequal fruit resources and categories of birds across these habitats were tested by χ^2. Abundance of fruit-bearing plants by habitat and the association of plant abundance with fruit eating birds and seeds recovered were tested by χ^2. Correlation between all fruit-eating bird species present and seeds recovered from ingested fruit was tested by Spearman Rank Correlation (r_s). Statistically significant differences were indicated at $P \leq 0.05$. StatView Student (Abacus Concepts 1991) package for the Macintosh computer and Statistics for Ornithologists (Fowler and Cohen 1995) were utilized for analyses.

RESULTS

In the 60 net spans and 11,499 net hr of effort used for the comparisons 4,827 birds of 93 species were captured during 170 weekly sample days in September and October 1979–1997 (Table 1). September was the peak of migrant species diversity (Suthers et al., unpubl. data); late October was the peak of migration (Leck 1972).

Bird use during long term successional changes.—Between 1979 and 1993 a shrub-tree interface (Lane 2E) succeeded into a young woodland. The number of birds captured in the interface ($n = 286$) declined significantly over time from 86 b/100 nh in 1979 to 8 b/100 nh in 1993 (linear regression: $R^2_{adj} = 0.33$, $F = 20.26$, 1 df, $P < 0.001$). By comparison, an open shrubland (Lane 2X) succeeded to dense shrubland and the number of birds captured ($n = 554$) did not change over time (50 b/100 nh in 1979 and 46 b/100 nh in 1993; linear regression: $R^2_{adj} = 0.0003$, $F = 1.01$, 1 df, $P > 0.05$).

Between 1982 and 1985 a black walnut (*Juglans nigra*) invasion of a multiflora rose shrubland (Lane 10X) had shaded out the shrubs and created an open understory with a shade tolerant forb cover. Bird captures ($n = 93$) declined significantly in the 4 years from 68 b/100 nh in 1982, to 4 b/100 nh in 1985 (linear regression: $R^2_{adj} = 0.61$, $F = 18.13$, 1 df, $P = 0.002$). In comparison, an open multiflora rose shrubland (Lane 10) expanded to a dense shrubland between 1982 and 1985 but the number of birds captured ($n = 267$) remained the same over the 4 years (104 b/100 nh vs 76 b/100 nh; linear regression: $R^2_{adj} = 0.23$, $F = 4.32$, 1 df, $P > 0.05$).

Between 1984 and 1993 a tree invasion shaded out a dense shrubland (Lane 3), forming a young woodland. Birds captured ($n = 285$) in the invaded shrubland declined significantly from 39 b/100 nh in 1984 to 7 b/100 nh in 1993 (linear regression: $R^2_{adj} = 0.135$, $F = 6.67$, 1 df, $P = 0.014$). In comparison, an intermediate shrubland (Lane 2) succeeded into a wooded shrubland and birds captured ($n = 928$) between 1979 (27 b/100 nh) and 1993 (31 b/100 nh) did not change (linear regression: $R^2_{adj} = -0.02$, $F = 0.06$, 1 df, $P > 0.05$).

Bird use of contrasting successional stages, short term.—In 1989 and 1992–1993 a wooded shrubland (Lane 2 above, including the dense shrubland extension Lane 2X) was compared with the young woodland (Lanes 3 and 3X above). Birds used the shrubland (582 captures) more frequently than the woodland (149 captures; $n_1 = 21$, $n_2 = 21$, $U = 36$, $P < 0.001$).

In 1994 a wooded shrubland (center Lanes 4 and 4S) and a young mixed deciduous woodland (north Lanes 4 and 4S) were compared. Birds used the shrubland (97 captures) more frequently than the woodland (11 captures; $n_1 = 7$, $n_2 = 7$, $U = 4.5$, $P = 0.01$).

Each taxonomic family had more birds in the shrublands than in the woodlands except Turdidae, which was similarly distributed (Table 2). Similarly when analyzed by migratory strategy, shrubland was used more often than

TABLE 2. Autumn migratory bird captures in shrublands and young deciduous woodlands in central New Jersey during 1989, 1992–1994. Captures are categorized by family and migratory strategy.

	Species	Shrubland captures	Woodland captures	χ^2
Family[a]				
Cardinalidae	3	27	3	19.20
Fringillidae	3	25	0	25.00
Emberizidae	8	141	2	135.11
Vireonidae	3	24	2	18.62
Parulidae	22	126	63	21.00
Mimidae	1	137	13	102.51
Regulidae	2	81	12	51.19
Paridae	3	50	16	41.76
Turdidae	5	36	28	1.00
Migratory strategy[b]				
Neotropical migrant	30	155	82	22.49
Short-distance migrant[c]	14	406	50	277.93
Permanent resident	8	116	28	53.78

[a] χ^2 tests, 1 df, $P < 0.001$ in all except Turdidae which were similarly distributed, $P > 0.05$.

[b] χ^2 tests, 1 df, $P < 0.001$, except the short-distance migratory Yellow-rumped Warbler which was distributed 10:10 in shrublands and woodlands and the Neotropical thrushes which were distributed 17:21, $P > 0.05$.

[c] Gray Catbirds (Mimidae) categorized here as short-distance migrants, could be considered Neotropical migrants.

woodland by Neotropical migrants, short distance migrants, and residents. Exceptions were four Neotropical migratory thrush species and short distance migratory Yellow-rumped Warbler (*Dendroica coronata*) that were equivalently represented in both habitats (Table 2).

Bird use of shrublands with disproportionate fruit resources.—Comparison of birds in three wooded shrublands (Lanes 2, 3R, and 10) resulted in 1575 captures of 35 families and 77 species (Table 3). Bird use was dissimilar. The panicled dogwood shrubland (Lane 2) was the most heavily used and the multiflora rose/vine shrubland (Lane 10) the least used by passage migrants during 1989–1991 ($\chi^2 = 31$, 2 df, $P < 0.001$). By 1995–1997 vines, most abundant in the multiflora rose/vine shrubland, had matured and fruited, and captures of passage migrants became equivalent in the multiflora rose/vine shrubland and the panicled dogwood shrubland, each higher than in the red cedar shrubland (Lane 3R; $\chi^2 = 10$, 2 df, $P = 0.006$). This change was mainly due to an influx of White-throated Sparrows (*Zonotrichia albicollis*) and Yellow-rumped Warblers in the multiflora rose/vines shrubland.

Although the short-distance migratory emberizids preferred the rose/vine shrubland (Table 3), the Eastern Towhee (*Pipilo erythrophthalmus*) was more abundant in the panicled dogwood shrubland ($\chi^2 = 7$, 2 df, $P = 0.03$). The Neotropical *Catharus* thrushes were not distributed differently ($\chi^2 = 2$, 2 df, $P > 0.05$), but the short-distance migratory Hermit Thrush (*Catharus guttatus*) was more common in the panicled dogwood shrubland ($\chi^2 = 8$, 2 df, $P = 0.019$). The Neotropical migratory Wood Thrush (*Hylocichla mustelina*) was more abundant in the rose/vine shrubland ($\chi^2 = 10$, 2 df, $P = 0.006$). Of the resident parids, the Tufted Titmouse (*Baeolophus bicolor*) favored the panicled dogwood shrubland ($\chi^2 = 22$, 2 df, $P < 0.001$), the Black-capped Chickadee (*Poecile atricapillus*) favored the red cedar shrubland ($\chi^2 = 14.11$, 2 df, $P < 0.001$), and the Carolina Chickadee (*P. carolinensis*) favored the rose/vines shrubland ($\chi^2 = 13.93$, 2 df, $P < 0.001$).

Defecated or regurgitated samples were deposited in the holding boxes by 431 birds of 77 species captured during 1995–1997. Evidence of fruit and seeds from ingested fruit was present in 333 samples (77%) from 42 species. Individuals of six additional species that were captured but left no evidence of eating fruit were observed eating fruit during the study. Altogether, 48 species (62%) of the 77 species captured had eaten fruit.

Equivalent numbers of individuals of the 42 fruit eating species were captured in the pan-

TABLE 3. Comparative mist-net captures in three wooded shrublands in central New Jersey with varying proportions of fruiting plant species. 1989–1991, 1995–1997. Dominant shrubs were panicled dogwood (*Cornus racemosa*) in Lane 2, red cedar (*Juniperus virginiana*) in Lane 3R, and multiflora rose (*Rosa multiflora*) in Lane 10.

	Birds captured				
	L2	L3R	L10	χ^2	P
Total captures 1575 birds	568	428	579	27.00	<0.001
Strategy					
Migrants, 1296 birds	470	343	483	27.70	<0.001
Residents, 279 birds	98	85	96	1.05	>0.05
Neotropical migrants, 7 families, 355 birds	131	89	135	10.98	0.004
Parulidae, 19 species	97	71	104	6.67	0.04
Turdidae[a], 5 species	13	9	17	2.46	>0.05
Vireonidae[b], 3 species	10	5	5	2.50	>0.05
Tyrannidae, 5 species	9	2	4	5.20	>0.05
Small samples combined: Cuculidae 2 sp., Trochilidae 1 sp., Thraupidae 1 sp.	2	2	5		
Short-distance migrants, 14 families, 941 birds	339	254	348	17.15	<0.001
Emberizidae, 7 species:	96	82	173	41.04	<0.001
Parulidae, 1 species[b]	33	42	35	1.22	>0.05
Mimidae[a], 2 species	106	52	56	25.38	<0.001
Troglodytidae, 2 species	7	5	14	5.15	>0.05
Regulidae, 2 species	52	46	50	0.38	>0.05
Turdidae[a], 2 species	28	20	12	6.40	0.04
Small samples combined: Scolopacidae 1 sp., Accipitridae 1 sp., Picidae 1 sp., Tyrannidae 1 sp., Certhiidae 1 sp., Vireonidae 1 sp., Icteridae 1 sp., Fringillidae 1 sp.	17	7	8	5.69	>0.05
Residents, 14 families, 279 birds	98	85	96	1.05	>0.05
Cardinalidae, 1 sp.	9	22	22	6.38	0.04
Emberizidae, 1 sp.	4	2	11	7.88	0.02
Paridae, 3 species	69	49	50	4.54	>0.05
Small samples combined: Strigidae 1 sp., Columbidae 1 sp., Picidae 3 sp., Bombycillidae 1 sp., Sturnidae 1 sp., Corvidae 2 sp., Sittidae 1 sp., Mimidae 1 sp.. Turdidae 1 sp., Fringillidae 1 sp.	16	12	13	0.63	>0.05

[a] Primary frugivores.

[b] Secondary frugivores (see Blake and Hoppes 1986).

icled dogwood shrubland and rose/vines shrubland and fewer were captured in the red cedar shrubland ($\chi^2 = 25.10$, 2 df, $P < 0.001$; Table 4). The number of species of fruit eaters did not differ by migratory strategy ($\chi^2 = 1.85$, 2 df, $P > 0.05$). Most of the individuals were short distance migrants ($\chi^2 = 276.9$, 2 df, $P < 0.001$), strongly represented by the Gray Catbird (*Dumetella carolinensis*), Yellow-rumped Warbler, and American Robin (*Turdus migratorius*).

Equivalent numbers of individuals of the 28 non-fruit eating species were captured in the panicled dogwood shrubland and the red cedar shrubland but more were captured in the multiflora rose/vine shrubland ($\chi^2 = 7.28$, 2 df, $P = 0.026$). The highest number of non-fruit eating species were Neotropical migrants ($\chi^2 = 16.36$, 2 df, $P < 0.001$). Neotropical migrants also had the most individuals ($\chi^2 = 87.54$, 2 df, $P < 0.001$), strongly represented by warblers (Parulidae) with 13 species and 64 individuals.

The most frequent evidence of fruit consumption was recovered from Gray Catbirds ($n = 86$), Yellow-rumped Warblers ($n = 55$), American Robins ($n = 41$), Hermit Thrushes ($n = 21$), and White-throated Sparrows ($n = 11$), accounting for 67% of the positive samples. They took all of the 12 major fruit spe-

TABLE 4. The number of fruit-bearing plants next to the net lanes 1992–1997, and the average number of seeds recovered from 333 birds of 42 species that had eaten fruit, 1995–1997 in shrublands of similar successional stages in central New Jersey.

	Fruit-bearing plants					Seeds ingested[a]		
Plants	L2	L3R	L10	χ^2	P	Lane 2	Lane 3R	Lane 10
Panicled dogwood *Cornus racemosa*	42	28	1	37	<0.001	0.6 Catbird 1**[b] Hermit Thrust 1***	0.1 Catbird 0.2	0.1 Catbird 0.2
Autumn-olive *Eleagnus umbellata*	5	22	1	8	<0.05	1 Catbird 1*** Robin 2	0.2 Catbird 1 Robin 0.2	0.1 Catbird 0.2 Cardinal 1**
Red cedar *Juniperus virginiana*	6	24	0	31	<0.001	0.01 Catbird 0.04	1 Robin 2***	0.1 Y-r Warbler 0.1
Multiflora rose *Rose multiflora*	30	26	112	84	<0.001	0.2 Mockingbird 1	1 Hermit Thrush 6***	0.4 Mockingbird 5
Virginia creeper *Parthenocissus quinquefolia*	4	2	2	1	>0.05	0.3 Gray-c Thrush 3	0.4 Robin 1*	0.3 Hermit Thrush 1
Frost grape *Vitis vulpina*	1	1	24	41	<0.001	0.1 Catbird 0.1	0.2 Purple Finch 3	0.1 Robin 0.4***
Japanese honeysuckle *Lonicera japonica*	7	4	10	3	>0.05	0.1 Wood Thrush 2	0.2 Hermit Thrush 3	0.1 Y-r Warbler 2***
Poison ivy *Toxicodendron radicans*	1	1	4	3	>0.05	0.2 Y-r Warbler 1 W-t Sparrow 1	0.5 Y-r Warbler 3 Purple Finch 3	1 Y-r Warbler 4*** W-t Sparrow 1
Other plant species	8	6	4	1	>0.05	0.5	0.2	0.1
Totals, all plants	97	111	150	12	<0.01			

Birds	Lane 2	Lane 3R	Lane 10
Total birds of 42 fruit eating species in each lane	135	68	130
Total birds eating shrub fruit	125	55	108
Number of shrub seeds recovered	194	126	78
Correlation (r_{Sp}) between birds and shrub seeds[c]	0.78***	0.77***	0.70***
Total birds eating vine fruit	104	63	119
Number of vine seeds recovered	84	96	387
Correlation (r_{Sp}) between birds and vine seeds[c]	0.56**	0.82***	0.78***

[a] Average number of ingested seeds recovered in a given lane, the species that ate the most, and the average number of seeds taken by that species. Species specific data on fruits taken by birds are available from the first author.

[b] P values, χ^2 contingency coefficient of association, plant species abundance, bird species abundance, average number of seeds recovered.

[c] P values, Spearman's correlation coefficient (r_{Sp}) birds, average number of seeds recovered.

* $P < 0.05$, ** $P < 0.001$, *** $P < 0.0001$.

cies available. Purple Finches (*Carpodacus purpureus*, *n* = 5), Northern Cardinals (*Cardinalis cardinalis*, *n* = 13), and Tufted Titmice (*n* = 5) each took up to 10 species of fruit.

Fecal and regurgitated samples yielded up to four fruit species simultaneously in individual catbirds, up to three species of fruit in robins, and up to two species of fruit in Wood Thrushes and Hermit Thrushes. Virtually no insects were in samples from the primary frugivores, Gray Catbird and American Robin. A few insects were in samples with fruit from the *Hylocichla* and *Catharus* thrushes, Cedar Waxwings, Yellow-rumped Warblers, and Red-eyed Vireos (*Vireo olivaceus*). Insects mixed with some fruit were in samples from secondary frugivorous birds, Willow Flycatchers (*Empidonax trailii*), White-eyed Vireos (*Vireo griseus*), and Common Yellowthroats (*Geothlypis trichas*). Fecal samples that lacked fruit contained insect parts and/or undetermined pulverized matter (possibly seeds). Feces at daybreak, before birds could feed, were chalky.

The order, timing, and duration of fruit species consumed by birds agreed with observations of fruit availability. Fruit availability differed in the three shrublands (Table 4). In some cases there was a significant association between availability of a fruit species in a habitat, a bird species most numerous in that habitat, and the average number of seeds recovered from that bird (Table 4). Gray Catbirds in the panicled dogwood shrubland (55 samples) took 48% autumn-olive, 30% panicled dogwood, 12% multiflora rose, and smaller amounts of Virginia Creeper, fox grape, poison ivy and red cedar. Catbirds in the other two shrublands (31 samples) took 21% each autumn olive and multiflora rose, 15% poison ivy, 14% Virginia creeper, 12% panicled dogwood, 9% frost grape, and some Japanese honeysuckle and red cedar. Hermit Thrushes in the panicled dogwood shrubland (5 samples), took 56% panicled dogwood, 33% multiflora rose, and 11% autumn-olive. In the other shrublands (16 samples), they took 55% Japanese honeysuckle, 22% multiflora rose, 10% Virginia creeper, and smaller amounts of panicled dogwood, red cedar, frost grape, poison ivy and autumn-olive. The 4 Neotropical *Catharus* thrushes in the panicled dogwood shrubland (12 samples) took 23% each of panicled dogwood and Virginia creeper, and 54% Japanese honeysuckle. In the other shrublands (3 samples) they took Virginia creeper and Japanese honeysuckle. Wood Thrushes in the panicled dogwood shrubland (5 samples), took 60% Japanese honeysuckle, 25% panicled dogwood, 10% autumn-olive, and 5% frost grape, and in the other shrublands (2 samples) took dogwood, autumn-olive and grape. House Finches (*Carpodacus mexicanus*) in the panicled dogwood shrubland (4 samples) took 67% autumn-olive and 33% poison ivy. White-throated Sparrows in the panicled dogwood shrubland (6 samples) and rose/vine shrubland (5 samples), took 44% and 31% poison ivy respectively, and 12% each of Virginia creeper and autumn-olive.

Yellow-rumped Warblers in the rose/vines shrubland (45 samples), took 59% poison ivy, and 38% Japanese honeysuckle. In the red cedar shrubland (7 samples) they took 88% poison ivy and smaller amounts of red cedar, Virginia creeper, and frost grape. American Robins (41 samples) in the red cedar and multiflora rose/vine shrublands took 46% red cedar, 29% Virginia creeper, 9% autumn-olive, 8% frost grape, and smaller amounts of multiflora rose, Japanese honeysuckle, panicled dogwood, and poison ivy. Cedar Waxwings (*Bombycilla cedrorum*) in the red cedar shrubland (3 samples) took 80% red cedar and 10% each frost grape and multiflora rose. In late October 112 birds of 20 species took 38% poison ivy, 28% grapes, 13% red cedar, and smaller amounts of viburnum, multiflora rose, silky dogwood, and crab apples.

DISCUSSION

Habitat use by birds in the autumn differed according to the successional stage and vegetative composition of the habitat. The successional habitat most frequently used by autumn migratory songbirds was shrubland. Vegetation structure was important, and birds abandoned shrub habitats that were shaded out by invading trees.

The abundance and/or quality of fruits appeared to be the resource that attracted migrants. If successional stage and vegetation structure alone were important in choosing between shrubland and woodland, birds would have shown no preference among the three shrublands at similar successional stages; however, there was differential use of the shrublands. Not only did birds leave habitats as fruit-bearing shrubs became overgrown by trees, but they also increased their use of habitats as fruit resources increased. This influx of birds was seen especially in the increased use of the multiflora rose/vine shrubland as the vine fruits became available. The observation that autumn habitat choice was influenced by presence of fruit is consistent with the results of other studies. In a 600 ha forest plot 19 km NE from our study site, during an autumn Baird (1980) observed more birds and fruits along shrubby edges, clearings, and paths than in forest interiors. In central Illinois during 3 autumns Martin and Karr (1986) found more birds in forest light gaps with fruiting plants up to 3 m tall than in non-gap areas where vegetation cover up to 3 m had little fruit.

Only a few bird species captured in this study are not known to eat fruit. All but 6 of the captured 28 species lacking evidence of eating fruit have been shown to take some fruit, mostly in the autumn (Martin et al. 1951, Terres 1980, Ehrlich et al. 1988, Poole and Gill 1992, White 1989, Suthers 1988, Parrish 1997). The 6 species for which there is no evidence of fruit eating are Sharp-shinned Hawk (*Accipiter striatus*), Eastern Screech Owl (*Otis asio*), Ruby-throated Hummingbird (*Archilochus colubris*), Blue-winged Warbler, (*Vermivora pinus*), Worm-eating Warbler (*Helmitheros vermivorus*), and Winter Wren (*Troglodytes troglodytes*). With most species of small birds from many families taking fruit, it would seem that the trophic classification (Thompson and Willson 1979, Blake and Hoppes 1986) of most songbirds needs to be modified or qualified by season to include migration and winter diets.

As Hutto (1990) pointed out, it is hard to perceive food availability in the same manner as birds. Several factors possibly work together to explain why fruit resources should influence the choice of shrubland habitat. Birds shifted their diet with the changes in resource abundance from insects to fruit in September and October, based on fecal and regurgitated samples. Breeding season insectivores took fruit in the autumn even though arthropods, especially Orthoptera, Diptera, and Arachnida were abundant until early to mid-October. The change from an insect diet to a primarily fruit diet was especially evident in the Gray Catbird, which was present until mid-October, and in the Yellow-rumped Warbler, present from October into winter.

Concurrent ripening and size limitations (see White 1989 for gape sizes) may determine which fruits are consumed together. Bird species for which we have larger sample sizes were eating almost every species of fruit available in the sequence that it ripened. Stiles (1980, 1993) and Bairlein and Gwinner (1994) demonstrated that frugivorous birds chose high lipid fruits first. Their studies did not include the introduced autumn-olive (1.4% lipids, 62.7% carbohydrates; nutritional data are from White 1989), a major source of carbohydrates in this study. It was eaten by many birds together with panicled dogwood (33.5% lipids, 22.1% carbohydrates), the most abundant source of lipids in this study. Nor did these researchers include the introduced Japanese honeysuckle (1.6% lipids, 50.3% carbohydrates) which was taken in large quantities together with poison ivy (42% lipids, 0 carbohydrates, Stiles and White 1986). White (1989) also found that lipid-rich and lipid-poor fruits were used concurrently, perhaps to achieve a nutritional balance (White and Stiles 1983).

Digestive availability is a crucial factor in how a bird utilizes food resources, and digestive ability may change seasonally with changes in the resources (Levey and Karasov 1992, Karasov 1996). In addition to Yellow-rumped Warblers, which are known to digest the waxy poison ivy fruits (Place and Stiles 1992), 20 other species also took poison ivy berries. There was no evidence from fruit samples or observations that Cedar Waxwings took high-lipid fruit, although they are capable of digesting lipids (Martinez del Rio and Restrepo 1993). The poorer ability of American Robins to absorb digested lipids compared to Wood Thrushes (Zurovchak et al. 1999) could explain why the robins were more plentiful in the red cedar shrubland and partook of Virginia creeper (16.2% lipids, 19.4% carbohydrates), together with red cedar (7.2% lipids, 41.7% carbohydrate), frost grapes (1.6% lipid, 47.9% carbohydrate), and multiflora rose

(1.5% lipids, 55.1% carbohydrates), whereas the Wood Thrushes, Hermit Thrushes and Swainson's Thrushes (*Catharus ustulatus*) partook heavily of panicled dogwood and high-carbohydrate fruit in the panicled dogwood shrubland. Digestive physiology could explain why flocks of birds visiting the frost grapes did not appear to ingest large amounts. The American Robin and Gray Catbird cannot digest sucrose (Martinez del Rio 1990, Malcarney 1992), but they seemed to take grapes as often as the Cedar Waxwing that can digest sucrose (Martinez del Rio et al. 1989, 1992). A digestive constraint in grapes may be phenolics that impair digestion. One suggested remedy is to mix grapes with arthropod protein (Witmer 1994). The mix of insects and fruit by the waxwing and thrushes is consistent with this hypothesis.

Age and experience may influence autumn frugivory because fruit is easier for the young to obtain than insects. Most (79%) of all birds we captured were young of the year. Fruits may determine habitat use by birds because of their need for rapid deposition of fat for migratory fuel. In the autumn, insect protein (over 70% dry weight; Robel et al. 1995) is thought to be less important to grown juvenile birds than the fruit lipids and carbohydrates needed for building fat deposits prior to migration (Stiles 1980, Bairlein and Gwinner 1994). Bairlein and Simons (1995) indicated that a combination of some protein with high lipid fruits may be optimal for digestive assimilation and fat accumulation. Only 10% of the migrants we captured, most of which were adults, appeared to have fat loads that would enable them to continue the next night without further refueling time (Blem 1980, Biebach et al. 1986). Most of the migratory birds we captured needed to amass fat. The average fat score, though only roughly correlated with amount of fat present, was 1.2 on a scale of 1–3, indicating insufficient fuel to support a long journey over the Atlantic Ocean (Moore and Kerlinger 1987).

Successional old fields with a diversity of native fruiting shrubs and vines are an important resource to autumn migratory birds that need to refuel for their long journeys. Winker and coworkers (1992) and Weisbrod and coworkers (1993) in Minnesota reported the heavier use of swamp, floodplain, willow and oak habitats, sedge fen, pine forest, and alder swale compared to upland forest habitats. Parrish (1997) reported the importance of fruiting scrub habitat for autumn migrants on Block Island off the coast of Rhode Island. These findings emphasize the need to conserve successional shrublands and other diverse habitats in addition to forests in the northeastern U.S. Birds also utilize the shrubs during spring migration and the shrubland attracts its own community of breeding migrants (Suthers 1988) that are declining because of loss of habitat (see Askins 1998 for overview). Land managers should consider maintaining and enhancing existing native fruiting shrublands and edge habitats to insure that these resources remain available.

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Short Communications

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Age-specific Breeding in Emperor Geese

Joel A. Schmutz[1]

ABSTRACT.—I studied the frequency with which Emperor Geese (*Chen canagica*) of known age were observed breeding on the Yukon-Kuskokwim Delta, Alaska. No one- or two-year old geese were observed on nests. Three-year old geese bred at a lower rate than four-year old geese. These data suggest that patterns of age-specific breeding in Emperor Geese are similar to other sympatrically nesting, large bodied geese [Greater White-fronted Geese (*Anser albifrons*)] but delayed relative to smaller bodied geese [Cackling Canada Geese (*Branta canadensis minima*) and Pacific Black Brant (*B. bernicla nigricans*)]. *Received 23 Oct. 1999, accepted 5 Feb. 2000.*

Age-specific frequencies of breeding are of theoretical and applied interest. Age of first breeding reflects a trade-off between current and future reproduction (Viallefont et al. 1995) and thus is a key element in the evolution of demographic life histories (Stearns 1992). Ages of maturation and first breeding affect generation time, and place an upper bound on the rapidity with which populations can grow. All other demographic parameters being equal, a species with an earlier age of breeding will have a higher annual growth rate than a species that begins breeding at a later age (Stearns 1992).

Four species of geese breed sympatrically on the Yukon-Kuskokwim Delta (Y-K Delta), Alaska (Spencer et al. 1951). Black Brant (*Branta bernicla*) are the most thoroughly studied; occasional one-year olds breed, 72% of two-year olds, 73% of three-year olds, and at least 90% of four-year and older geese breed (J. Sedinger, unpubl. data). Although less rigorously quantified, Cackling Canada Geese *(B. canadensis minima*) exhibit similar patterns to brant (C. Ely, unpubl. data). Age of breeding of Greater White-fronted Geese (*Anser albifrons*) in northern Canada appears to be one year later than for brant (Warren et al. 1992); two-year old geese occasionally bred, but the mean age of breeding was greater than three years.

No previous researchers of Emperor Geese (*Chen canagica*) have examined age-specific breeding. Such information may prove valuable to understanding the evolved similarities and differences in life history between these four species of geese coexisting on the Y-K Delta. Differences in age-specific breeding between Emperor Geese and other Y-K Delta goose species could help explain why population growth rates observed for this species are lower than for other species (Petersen et al. 1994, Bowman et al. 1999). Here I document breeding by different age classes of Emperor Geese.

I conducted this study during 1993–1998 in a 90 km^2 area along the Manokinak River on the Yukon-Kuskokwim Delta, Alaska (61° 10′ N, 165° 10′ W). Each year, a crew of assistants and I rounded up flocks of flightless geese during their wing molt in late July and early August. Each captured goose was classified to sex and as either a gosling or an adult. We attached a standard Fish and Wildlife Service metal band and a plastic band with a unique alpha-numeric code to their tarsi. In late May and June of each year, we searched the same areas to locate nesting geese. When nesting geese were located, we used spotting scopes to scan their legs when they stood on the nest rim upon our approach. Geese originally banded as goslings and subsequently seen on nests constitute my sample for assessing age-specific breeding.

We banded 165 female goslings in 1993, 190 in 1994, and 125 in 1995. The younger age classes had progressively more opportunity to be observed nesting. In 1995 only two-year old geese were observable, in 1996 only two- or three-year old geese were observable,

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in 1997 only two-, three-, or four-year old geese were observable, and in 1998 five-year old and younger geese were observable. We never observed any one- or two-year old geese on nests. We observed a total of 3 three-year old, 7 four-year old, and 3 five-year old geese on nests. Four geese were observed on nests in multiple years; three as both four- and five-year olds and one as a three- and four-year old.

The principal conclusion from this study is that few (if any) two-year old geese breed and that three-year old geese breed at a lower frequency than older geese. The small sample sizes of this study necessitate a cautious interpretation. However, qualitatively, these patterns appear similar to those for Greater White-fronted Geese (Warren et al. 1992). In contrast, sympatric Black Brant and Cackling Canada Geese frequently breed at two years (72% of such brant) and numerous one-year old breeders have been documented (J. Sedinger, unpubl. data; C. Ely, unpubl. data). These interspecific differences are consistent with models describing positive relationships between body size and age at maturation (Stearns 1992). Adult female Greater White-fronted Geese (1809 g; Ely and Dzubin 1994) and Emperor Geese (1638 g; Petersen et al. 1994) are similar in mass when their eggs hatch and much larger than Black Brant (1025 g; Reed et al. 1998) and Cackling Canada Geese (1137 g; C. Ely, unpubl. data).

Life history theory predicts that interspecific differences in age-specific reproduction among potential competitors, as apparently occurs among geese on the Y-K Delta, should be accompanied by counter-balancing differences in survival and longevity (Stearns 1992). Interestingly, despite an earlier age of breeding, survival of Black Brant (Ward et al. 1997) was as high or higher than that observed for Greater White-fronted Geese (Schmutz and Ely 1999), Emperor Geese (Schmutz and Morse 2000), and Cackling Canada Geese (Raveling et al. 1992; Fowler and Ely, unpubl. data). These comparisons are complicated by differences in the time of study and effects of harvest; nonetheless, they suggest further examination of the comparative life histories of these sympatrically breeding species is warranted.

Since 1986 Greater White-fronted Geese and Cackling Canada Geese on the Y-K Delta have increased at average annual rates of about 11% and 14%, respectively (Bowman et al. 1999). I am unaware of population increases in geese more than 14% per annum, other than by immigration. Using models of Schmutz and coworkers (1997), the difference in population growth rates between these two species is approximately equivalent to a one year difference in age-specific breeding frequencies (i.e., model breeding frequencies of one-, two- and three-year old small-bodied geese as respectively equal to that for two-, three-, and four-year old large-bodied geese; Schmutz, unpubl. data). Although population growth in Emperor Geese is currently lower (Bowman et al. 1999, Eldridge and Dau 1999), the potential maximum sustained population increase of this species may be limited to that seen in Greater White-fronted Geese and not in Cackling Canada Geese, based on the species specific patterns in age-specific breeding.

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Winter Diets of Sandhill Cranes from Central and Coastal Texas

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ABSTRACT.—We determined diet composition of Sandhill Cranes (*Grus canadensis; n* = 136) wintering in 4 regions of Texas during November–January 1996–1997 based exclusively on examination of esophageal and proventricular contents. Wintering Sandhill Cranes were predominately herbivorous, with animal matter representing less than 5% of their diet. Agricultural grains comprised most of the diet of wintering Sandhill Cranes from all regions of Texas except the South Texas Plains where nut-grass (*Cyperus* spp.) tubers made up a larger proportion of their diet. Cranes used agricultural and native plant matter and animal matter in different proportions among regions. There were no sex or subspecific related differences in frequency of occurrence or proportional dry mass of foods consumed by wintering Sandhill Cranes. Agricultural foods represented a larger proportion of the diets of Sandhill Cranes in this study than in previous studies conducted along the Gulf Coast, probably because of improved sampling methodology and differences in habitat conditions. *Received 8 Oct. 1999, accepted 16 Feb. 2000.*

Diets of migrating and wintering Sandhill Cranes (*Grus canadensis*) from the mid-continental United States consist predominately (88–100% aggregate volume) of agricultural grains throughout most of their range (Iverson et al. 1982, Tacha et al. 1985, Walker and Schemnitz 1987). However, previous researchers on diet composition of Sandhill Cranes wintering in southern Texas found that these birds principally fed (94–100% aggregate volume) on native plant and animal matter (Guthery 1975, Hunt and Slack 1989). Hunt and Slack (1989) investigated winter diets of Sandhill Cranes at Aransas National Wildlife Refuge using fecal samples, and found that wolfberry (*Lycium virginiana*) fruits, live oak (*Quercus virginiana*) acorns, and insects were the predominant foods by volume and frequency of occurrence. Guthery (1975) documented Sandhill Crane food

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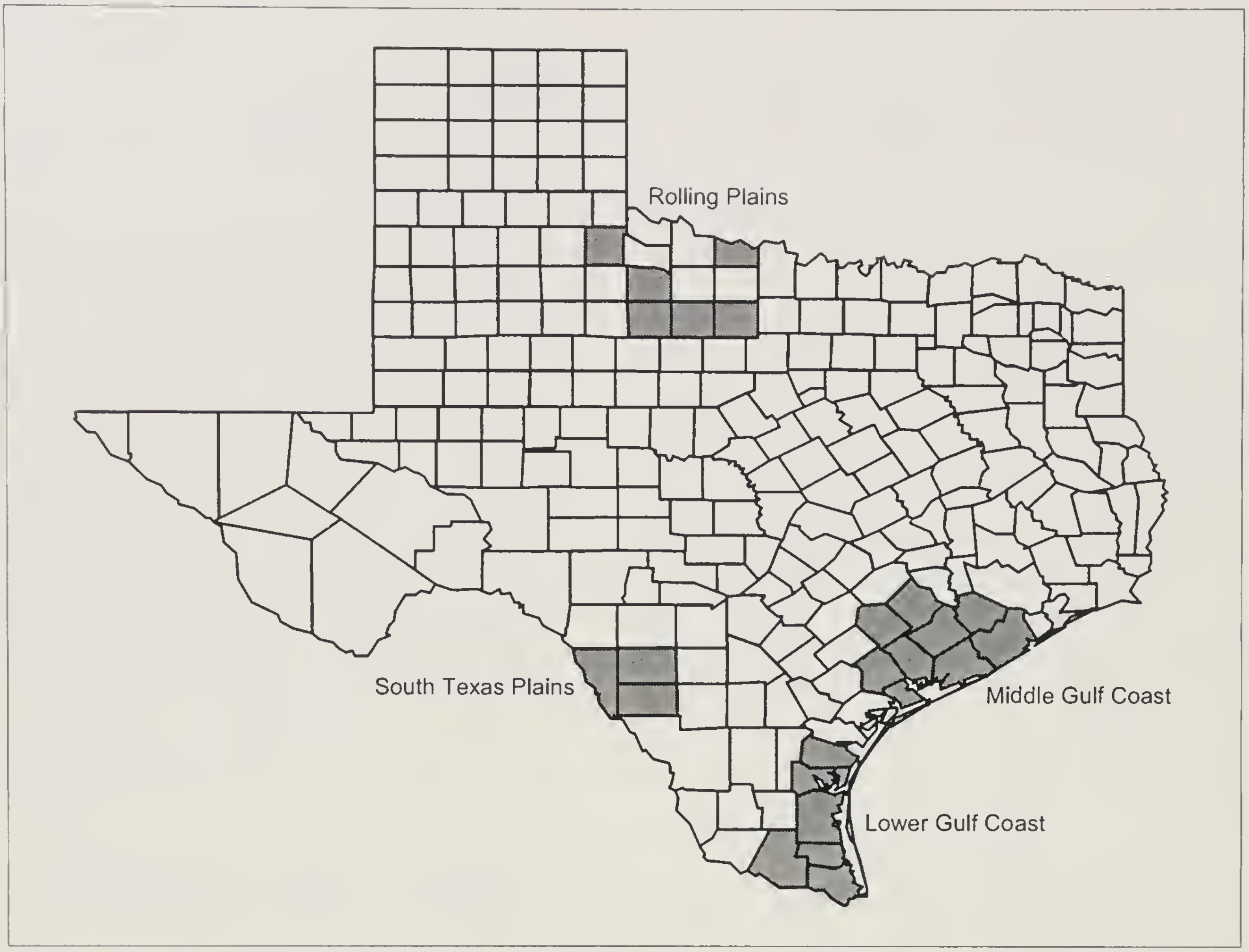

FIG. 1. Shaded areas indicate counties where Sandhill Cranes (*Grus canadensis*) were collected for diet composition analysis during November 1996–January 1997.

habits in coastal Texas using gizzard contents and found that native plant and animal matter comprised 91% of the diet. Additionally, Lewis (1974) determined diets of 20 Sandhill Cranes from the Mid-Coast of Texas using upper digestive tract contents and found that agricultural grains comprised a moderate proportion of their diet (60% total volume) relative to cranes wintering in other regions of Texas. Unfortunately, use of different and often biased methods in previous studies of crane food habits complicates comparison of results. Our objectives were to compare diets of Sandhill Cranes among 4 regions in Texas, including 2 regions for which no previous data exist (i.e., Rolling Plains and South Texas Plains), and to investigate variation in diet composition between sexes and among Sandhill Crane subspecies.

METHODS

We determined winter diets of After Hatch Year (AHY) Sandhill Cranes from the Mid- (n = 65) and Lower (n = 18) Coasts of Texas, South Texas Plains (n = 24), and Rolling Plains (n = 29) during November 1996–January 1997 (Fig. 1). Sandhill Cranes were collected by shooting as they returned to roost sites in the evening or as they left the roost sites in the morning. We attempted to randomly select specimens and collect no more than one crane per flock. Roosts were comprised of at least 30 flocks of cranes and flock size was variable. Flocks generally returned to roosts from many directions suggesting that they were feeding in different areas. We collected 10–20 cranes from each county (see Fig. 1) in each region; however, sample sizes were smaller in some counties in the Rolling Plains and South Texas Plains because of lower densities of cranes. Cranes were frozen as soon as possible after collection to minimize post-mortem digestion of foods. Specimens were sexed by gonadal examination. Discriminant models derived from measurements of AHY Sandhill Cranes of known sex and breeding origin (D. H. Johnson, unpubl. data) were used to partition our sample of cranes into Lesser Sandhill Cranes (*G. c. canadensis*), Canadian Sandhill Cranes (*G. c. rowani*), and Greater Sandhill Cranes (*G. c. tabida*), the 3 subspecies wintering in central and coastal Texas (Guthery and Lewis 1979, Tacha et al. 1986). Food contents were subsequently removed from the upper

TABLE 1. Percent occurrence and aggregate percent dry mass of foods consumed by Sandhill Cranes (*Grus canadensis*) in 4 regions of Texas during November 1996–January 1997.[c]

	% occurrence				Aggregate % dry mass			
Food item	Lower Coast (18)[a]	Mid-Coast (65)	Rolling Plains (29)	South Texas Plains (24)	Lower Coast (18)	Mid-Coast (65)	Rolling Plains (29)	South Texas Plains (24)
Total plant material	100	100	100	100	95.2	98.5	99.6	99.9
Agricultural plant material	88.9	53.8	86.2	62.5	82.8	49.5	85.8	49.7
Sorghum seeds (*Sorghum bicolor*)	88.9	1.5	24.1	12.5	82.8	1.5	23.6	7.8
Rice seeds (*Oryza sativa*)	0.0	36.9	0.0	0.0	0.0	34.3	0.0	0.0
Corn seeds (*Zea mays*)	0.0	16.9	6.9	20.8	0.0	13.4	6.9	20.8
Wheat seeds (*Triticum* spp.)	0.0	1.5	55.2	4.2	0.0	0.3	54.8	4.2
Wheat vegetation (*Triticum* spp.)	0.0	0.0	3.4	33.3	0.0	0.0	0.5	16.9
Native plant material	11.1	49.2	17.2	62.5	10.8	46.0	13.8	46.0
Nut-grass tubers (*Cyperus* spp.)	11.1	46.2	6.9	62.5	10.8	44.4	3.6	46.0
Acorns (*Quercus* spp.)	0.0	1.5	10.3	0.0	0.0	1.5	10.2	0.0
Spike rush seeds (*Eleocharis* spp.)	0.0	1.5	0.0	0.0	0.0	tr[b]	0.0	0.0
Unidentified roots	11.1	3.1	0.0	4.2	1.6	3.0	0.0	4.2
Unidentified vegetation	0.0	4.6	0.0	4.2	0.0	tr	0.0	0.3
Total animal material	50.0	10.8	31.0	20.8	4.8	1.5	0.4	0.1
Insecta	38.8	9.2	31.0	16.7	1.1	1.3	0.1	tr
Coleoptera	11.1	4.6	24.1	8.3	0.5	0.3	tr	tr
Adult beetles	0.0	3.1	17.2	4.2	0.0	tr	0.1	tr
Larval beetles (Dascillidae)	11.1	1.5	13.8	4.2	0.5	0.3	tr	tr
Orthoptera	27.8	6.2	20.7	8.3	tr	1.0	0.1	tr
Cricket (Gryllidae)	27.8	0.0	0.0	4.2	tr	0.0	0.0	tr
Grasshopper (Acrididae)	0.0	6.2	20.7	4.2	0.0	1.0	0.1	tr
Moth (Lepidoptera)	0.0	0.0	6.9	0.0	0.0	0.0	tr	0.0
Unidentified insects	5.6	1.5	3.4	8.3	tr	tr	tr	tr
Mollusca	11.1	1.5	3.4	4.2	3.7	0.1	tr	tr
Snail (Planorbidae)	0.0	1.5	3.4	0.0	0.0	0.1	tr	0.0
Unidentified shell fragments	11.1	0.0	0.0	4.2	3.7	0.0	0.0	tr

[a] *n* in parentheses.

[b] tr = < 0.1%.

[c] Inorganic material excluded from samples.

digestive tract (i.e., esophagus and proventriculus) of each bird and individually stored in 80% ethanol. Contents from the gizzard were not included because of potential biases associated with different passage rates of food items through this organ (Swanson and Bartonek 1970). Contents from each upper digestive tract were later identified, sorted, and oven dried to constant mass at 75–80° C.

Diets of wintering cranes were quantified as frequency of occurrence and aggregate percent dry mass for each food. Dry mass was selected to evaluate dietary importance of foods instead of volumetric measurements to provide a better basis for nutritional interpretation of the diet (Reinecke and Owen 1980). χ^2 analysis was used to test for differences in frequency of occurrence of food items among regions, subspecies of cranes, and between sexes (SAS Institute 1997). We investigated variation in aggregate percent dry mass of foods among regions, subspecies, and between sexes using Kruskal-Wallis 1-way analysis of variance tests (SAS Institute 1997). We then used a Dunn's multiple comparison test (Zar 1996: 227) to determine where differences occurred if the results of the Kruskal-Wallis test were significant. All analyses were made using SAS, version 6.12 for an IBM.

RESULTS

We collected 251 AHY Sandhill Cranes of which 136 (54%) contained food in their upper digestive tracts (Table 1). Subspecific and gender composition of cranes that contained food included 76 Canadian Sandhill Cranes, 33 Lesser Sandhill Cranes, and 27 Greater Sandhill Cranes, and 86 males and 56 females.

Plant materials (predominately agricultural plants and mostly grains) were the primary foods consumed in each region (Table 1). Sorghum (*Sorghum bicolor*) seeds were consumed in all regions, ranging from 83% of the diet in the Lower Coast to 24% in the Rolling Plains where wheat (*Triticum* spp.) seeds predominated the diet (55%); 34% of the diet of cranes from the Mid-Coast consisted of rice (*Oryza sativa*) seeds (Table 1).

Native plant material [nut-grass tubers, acorns, and spike-rush seeds (*Eleocharis* spp.)] represented almost half of the diet of cranes from the Mid-Coast and South Texas Plains, but less than 14% of the diet of cranes from the Lower Coast and Rolling Plains. In particular, nut-grass tubers had been consumed by approximately half of the birds collected from the Mid-Coast and South Texas Plains and represented 44% and 46% of their diets, respectively (Table 1). Nut-grass tubers comprised the largest proportion of any native food in the diet of cranes in each region except the Rolling Plains where acorns (10%) represented a larger fraction of the diet (Table 1).

Animal material consumed by wintering Sandhill Cranes consisted exclusively of insects and mollusk shells. Animal material never represented more than 5% of the aggregate dry mass of crane diets in any region; however, 50% of the cranes collected along the Lower Coast had ingested animal material (Table 1). Insects, particularly adult and larval beetles (Coleoptera), crickets (Gryllidae), and grasshoppers (Acrididae) were the most frequently ingested animals in all regions. Mollusk material in the diet of cranes consisted entirely of empty shells and shell fragments rather than whole organisms.

The frequency of consumption of plant material relative to animal material differed among regions (χ^2 = 8.46, 3 df, P = 0.04), as did agricultural and native plant material (χ^2 = 13.58, 3 df, P = 0.004). The proportional dry mass of plant and animal material in diets differed (χ^2 = 13.8, 3 df, P = 0.003) among regions, with cranes along the Lower Coast consuming a higher (Q = 2.56, P = 0.01) proportion of animal matter than cranes from the Mid-Coast. Sandhill Cranes used native plant material in different (χ^2 = 18.90, 3 df, $P < 0.001$) proportions among regions, with native plant material representing a larger proportion of the diet of cranes from the Mid-Coast and South Texas Plains than the diets of birds from the Lower Coast (Q = 2.55, P = 0.011; Q = 2.46, P = 0.014, respectively) and Rolling Plains (Q = 3.0, P = 0.002; Q = 2.75, P = 0.006, respectively). Agricultural plant material was consumed in different (χ^2 = 9.46, 3 df, P = 0.024) proportions among regions; Sandhill Cranes from the Rolling Plains ingested a greater proportion of agricultural plant material than cranes from the Mid-Coast (Q = 2.23, P = 0.026) and South Texas Plains (Q = 2.31, P = 0.021; Table 1).

The frequency with which agricultural, native plant, and animal materials occurred in Sandhill Crane diets within regions did not differ between sexes (all $P > 0.05$) or among subspecies (all $P > 0.05$). Additionally, there were no differences between sexes (all $P > 0.05$) in proportional dry-mass of animal, native plant, and agricultural plant material in their diets within regions, nor were there any differences among subspecies (all $P > 0.05$), except along the Lower Coast (χ^2 = 6.29, 2 df, P = 0.043) where native plant material represented a larger proportion (Q = 2.32, P = 0.023) of the diet of Lesser Sandhill Cranes than of Greater Sandhill Cranes.

DISCUSSION

Sandhill Cranes wintering in central and coastal Texas were principally herbivorous with animal matter comprising less than 5% of the diet, which is similar to diets of migrating and wintering Sandhill Cranes from other areas in mid-continent North America (Iverson et al. 1982, Tacha et al. 1985, Walker and Schemnitz 1987). Contrary to previous studies of Sandhill Crane food habits along the Gulf Coast (Guthery 1975, Hunt and Slack 1989), we found that agricultural foods were a large component in the diet. Wintering Sandhill Cranes apparently exploited readily available plant foods with high levels of digestible energy (e.g., rice, sorghum, wheat, and nut-grass tubers). Where agriculture plant material comprised lower proportions of the diet, consumption of nut-grass tubers increased.

The difference in proportional dry mass of animal material between the diets of cranes from the Lower and Mid-Coasts is the result of cranes from the Lower Coast ingesting more mollusk shell fragments. Lewis (1974) observed snail shells in crane gizzards from coastal Texas and attributed this to cranes picking up shell fragments as grit. The diet of cranes from the Lower Coast was the least diverse of all regions and may have resulted in specific nutritional deficiencies. Reinecke and Krapu (1986) suggested that mollusks and other invertebrates provide nutrients to compensate for protein and calcium deficiencies of agricultural grains during spring migration. The importance of animal matter in the diet of migrating Sandhill Cranes was evident from time budget observations that indicated that cranes spent the same amount of time obtaining animal material (3% of their diet) as they did to obtain corn (97% of their diet; Reinecke and Krapu 1986).

Similar to our findings, Tacha and coworkers (1992, 1994) reported that diets of male and female Sandhill Cranes from other areas in central North America were the same during migration and winter. Sandhill Cranes provide extended bi-parental care for their offspring and the family functions as a single unit throughout the first 10–11 months after the young hatch (Tacha et al. 1992, 1994). Therefore, similarities in diet between sexes and age classes are likely. However, our sample sizes were relatively small for some sex and subspecies classes within regions.

Previous research on Sandhill Crane diet composition along the Gulf Coast of Texas indicated that the cranes relied primarily on natural foods throughout the winter (Guthery 1975, Hunt and Slack 1989). However, differences in techniques used to analyze diet composition in those studies and the corresponding biases toward food items that remain identifiable in the gizzard and feces need to be considered when comparing results. Other factors that may affect diet composition of Sandhill Cranes in Texas include temporal distribution of foods and annual habitat variation. Guthery (1975) obtained 63% of his samples in February and March when sorghum may have been depleted in southern Texas (Ballard and Tacha 1994). Guthery's (1975) sampling period during winter 1971–1972 coincided with above normal (98% higher) precipitation following Hurricane Fern in September 1971. Sorghum is the predominant grain crop in southern Texas and the availability of waste grain is influenced by precipitation (Ballard and Tacha 1994). During years of above normal precipitation, the amount of grain available can be depleted by early winter through decomposition and germination. During dry years, waste grain can remain available throughout winter. Precipitation amounts along the Lower and Mid-Coasts during 1996–1997 averaged about 7% higher than the long-term average (NOAA 1999).

It is evident from our study that there is probably no marked difference in use of agricultural grains by cranes wintering in coastal Texas compared to those wintering in other areas of mid-continental North America. Sandhill Cranes exploit readily available, high energy foods during migration and throughout winter, but annual variation in habitat conditions can affect food availability. Agricultural grains are important when they are available, but cranes are not limited to agricultural grains and can alter their foraging behavior to obtain high-energy native foods.

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Food Habits of Cattle Egrets on St. Croix, U.S. Virgin Islands

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ABSTRACT.—Cattle Egrets (*Bubulcus ibis*) expanded their range greatly during the twentiethth century, making localized food habit studies necessary to determine their impact in newly invaded ecosystems. We examined 44 Cattle Egret stomachs collected in January 1993 from Alexander Hamilton Airport on St. Croix Island, U.S. Virgin Islands. Orthopterans and lepidopterans were the most prevalent invertebrate food items. The St. Croix anole (*Anolis acutu*) was the major vertebrate prey. Meat scraps and ticks occurred in minor quantities. *Received 29 March 1999, accepted 5 Jan. 2000.*

The adaptability of Cattle Egrets (*Bubulcus ibis*) has allowed them to expand their populations from northern South America (A.O.U. 1998) to Canada (Buerkle and Mansell 1963). Cattle Egrets were first reported on St. Croix Island in 1955 (Seaman 1955) and 1500–2000 birds currently inhabit the island (Boyd and Hall, unpubl. data). Because of their opportunistic feeding behavior, studies on localized food habits are important to determine potential effects on vertebrate and invertebrate prey communities. For example, in Queensland, Australia, several species of lizards, northern dwarf tree frogs (*Litoria fallax*), and young marine toads (*Bufo marinus*) are common prey items, although orthopterans are the major prey (McKilligan 1984). Similarly, in northern Florida, orthopterans are the major food item during June and July (Fogarty and Hetrick 1973). In South Africa, lepidopterans were the major prey from December to March, but annelids made up 44.5–67.5% of the prey from April to September (Siegfried 1971). Based on the stomach contents of 1 bird collected on St. Croix in February, Seaman (1955) reported that 92% of the contents were orthopterans, 6% were unidentified arachnids,

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and 2% were carabid beetles. Because information on the dietary habits of Cattle Egrets in the Virgin Islands is limited and because of potential impacts on endemic species, we identified and quantified the dietary components of Cattle Egrets during the winter on St. Croix Island.

STUDY AREA AND METHODS

We collected Cattle Egrets on St. Croix Island, a 212 km^2 island located 64 km south of St. Thomas. The birds were shot at Alexander Hamilton Airport (17° 42′ N, 64° 48′ W) as part of an ecological study conducted to supplement a wildlife hazard management plan. The flock, approximately 500 birds, was located in a mangrove stand east of the runway. Forty-four birds (24 males, 19 females, and 1 unknown sex) were collected on the afternoons of January 21–23, 1993. We removed the stomachs and preserved the contents in 10% formalin. We classified insect, centipede, and spider prey at the ordinal level (Borror and Delong 1964). Ticks (suborder Acarina) were identified to species, and the condition of the hypostome (mouthpart) was noted. We identified vertebrates to species (MacLean 1982; Schwartz and Henderson 1985, 1991). Some reptiles could only be identified to genus because of advanced decomposition. Abundance of prey items was determined for each bird. Because invertebrates rarely remain intact during digestion, we chose a particular body part (e.g., thorax of lepidopterans and arachnids) to determine abundance. We determined volume by water displacement after soaking formalized specimens in water for at least 24 hr. Using these data, we estimated relative frequency by abundance (number of individuals of a prey item/total number of individuals of all prey items ×100), volume (volume of a prey item/total volume of all prey items ×100), and occurrence (number of samples in which a prey item occurs/total number of samples ×100) and calculated an index of relative importance [(relative frequency by abundance + relative frequency by volume) × (relative frequency by occurrence/200); Findholt and Anderson 1995].

RESULTS AND DISCUSSION

We identified 11 invertebrate orders and 7 vertebrate species from 44 stomachs (Table 1). Invertebrates accounted for 53.5% of the volume of the stomach contents, with orthopterans, lepidopterans, and arachnids having the greatest volumes. Vertebrates, primarily the St. Croix anole (*Anolis acutus*), constituted 36.4% of the stomach volume, and meat scraps and unidentified matter constituted 10.1%.

Orthopterans, lepidopterans, and arachnids were the most frequent prey items in our samples. No lepidopterans occurred in the one Cattle Egret taken in February 1955 from St. Croix (Seaman 1955). However, lepidopterans are the major food item of Cattle Egrets in South Africa (Siegfried 1971). In Texas, orthopterans and arachnids frequently occur in the diet (Telfair 1983). In all of these studies, coleopterans, hymenopterans, hemipterans, dipterans, odonatans, and scolopendromorphan centipedes were of minor importance.

Other researchers reported that reptiles are not a major dietary component of Cattle Egrets (Snoddy 1969, Fogarty and Hetrick 1973, Telfair 1983, McKilligan 1984). In South Africa, vertebrates were more prominent in the diet during the wet season and early in the dry season (Siegfried 1971). The wet season on St. Croix begins in September and extends into December. *Anolis acutus* is the only *Anolis* species on the island (MacLean 1982) and occurred in 61.4% of the samples (Table 1). The common dwarf gecko (*Sphaerodactylus macrolepis*), a common species in the West Indies (MacLean 1982, Schwartz and Henderson 1991), occurred in 29.6% of the samples. The presence of these species suggests that Cattle Egrets likely forage in the taller vegetation or brushy habitats inhabited by these reptiles.

Only 1 mammalian species, the house mouse (*Mus musculus*), occurred in the stomachs, indicating that mammals are not a regular food item (Telfair 1983). Caribbean white-lipped frogs (*Leptodactylus albilabris*), Antillean frogs (*Eleutherodactylus antillensis*), Cuban treefrogs (*Osteopilus septentrionalis*), and marine toads were infrequent prey items. Meat scraps occurred in 6 (13.6%) samples, often in conjunction with dipterans. Previous researchers (Schwartz 1969, Pomeroy 1975, Burger and Gochfeld 1985) have suggested that Cattle Egrets eat insects concentrated at refuse sites.

Ticks occasionally were present in the stomach contents. We found 128 specimens of *Boophilus microplus* in 5 birds. It is uncertain whether these birds obtained ticks attached to the host (Telfair 1983). In a Florida study, no ticks were found in 841 Cattle Egret stomachs (Fogarty and Hetrick 1973). However in Texas, 2 Lone Star ticks (*Amblyomma americanum*) were recovered from 1000 boluses (Telfair 1983), and Snoody (1969) found that ticks comprised 0.1% of the prey items in the sum-

TABLE 1. Composition of the diet of Cattle Egrets from St. Croix Island (n = 44).

Prey items	Relative frequency by abundance[a]	Relative frequency by volume[b]	Relative frequency by occurrence[c]	Index of relative importance[d]
Insecta				
Orthoptera	15.9	18.6	72.7	12.5
Lepidoptera (adult)	21.8	15.8	70.5	13.2
Lepidoptera (larvae)	21.2	11.7	70.5	11.6
Hymenoptera	0.4	0.0	15.9	0.0
Diptera	7.9	1.7	54.5	2.6
Odonata	0.1	0.2	2.3	0.0
Coleoptera	0.1	0.2	9.1	0.0
Hemiptera	0.3	0.1	6.8	0.0
Chilopoda				
Scolopendromorpha	0.1	0.2	2.3	0.0
Arachnida				
Araneida	15.4	4.0	72.7	7.1
Acarina				
Boophilus microplus	3.7	1.1	11.4	0.3
Amphibia				
Leptodactylus albilaris	0.2	0.2	6.8	0.0
Osteopilus septentrionalis	0.2	0.4	11.4	0.0
Eleutherodactylus antillensis	0.0	0.1	2.3	0.0
Bufo marinus	0.0	0.1	2.3	0.0
Reptilia				
Anolis acutus	10.8	32.1	61.4	13.1
Sphaerodactylus macrolepis	1.6	1.7	29.5	0.5
Sphaerodactylus sp.	0.3	0.3	13.6	0.0
Mammalia				
Mus musculus	0.1	1.6	6.8	0.1
Other				
Meat scraps	t[e]	7.0	13.6	t
Unidentifiable matter	t	3.1	t	t

[a] RFN = (number of individuals of a prey item/total number of individuals of all prey items) × 100.
[b] RFV = (volume of a prey item/total volume of all prey items) × 100.
[c] RFO = (number of samples in which a prey item occurs/total number of samples) × 100.
[d] IRI = (RFN + RFV) × (RFO/200).
[e] t = trace.

mer diet of Georgia birds. The occurrence of a broken hypostome (mouthpart) or presence of cement cones (formed as a part of the attachment process) around a hypostome suggests tick removal from a host by Cattle Egrets (McKilligan 1984). Of 44 ticks selected randomly from boluses collected in Queensland, Australia, 3 had broken hypostomes, and 6 had cement cones. Using these criteria, we found that 107 (84%) ticks we observed likely had been removed directly from the host.

The Cattle Egret is an opportunistic feeder that has colonized many diverse habitats. Their adaptability to agricultural practices necessitates localized food habits to assess potential impacts. In our limited sample, we found no evidence that Cattle Egrets were consuming threatened or endangered vertebrates. However, because vertebrates were common in the diet of Cattle Egrets on St. Croix, additional studies with larger sample sizes are warranted.

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First Described Renesting Attempt by an American Bittern

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and Richard D. Crawford[5]

ABSTRACT.—Most life history traits of the American Bittern (*Botaurus lentiginosus*) have not been studied and are poorly understood. The ability of the American Bittern to renest has not been confirmed previously. A second nesting attempt by an American Bittern was observed on Agassiz National Wildlife Refuge on 8 July 1996. This information provides insight into American Bittern fecundity by showing that additional reproductive capability exists when nests are destroyed by predation or weather related events. Future studies of nesting bitterns will need to consider renesting when estimating density of nesting females.

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The American Bittern (*Botaurus lentiginosus*) is the most widely distributed wading bird in North America, breeding as far north as central Canada and wintering as far south as Central America (Bent 1926). Breeding Bird Survey results indicate a decline of 2.2%/year for American Bitterns survey-wide from 1966–1996 (Sauer et al. 1997). The American Bittern is listed as a migratory nongame bird of special concern by the U.S. Fish and Wildlife Service (1995) and is Blue-Listed by the National Audubon Society (Tate 1986).

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The paucity of knowledge regarding American Bittern life history has inhibited the implementation of effective management techniques to reverse the downward trend in American Bittern populations. In 1994, we initiated a study to investigate these life history traits. Phase II of the project (1996–1997) focused on estimating home-range size and habitat use by radio telemetry. Renesting by American Bitterns has been suspected (Svedarsky 1992), although not documented. We describe the renesting activities of a radio-marked American Bittern and provide nest site information.

STUDY AREA AND METHODS

Our study area, Agassiz National Wildlife Refuge (NWR; 48° 20′ N, 95° 55′ W), is located 17.7 km east of Holt, Minnesota, and contains 24,000 ha, including approximately 16,035 ha of restored wetlands. Most of the 18 impoundments are dominated by emergent vegetation consisting of cattail (*Typha* spp.), bulrush (*Scirpus* spp.), giant reed grass (*Phragmites australis*), sedge (*Carex* spp.), and willow (*Salix* spp.) Water depths rarely exceed 2 m and average approximately 1 m during summer. The population of American Bitterns on Agassiz NWR has been estimated at 384 ± 72 (L. Bennett, unpubl. data).

Mist nets and dip nets were used to capture female American Bitterns (Brininger 1996). Captured birds were fitted with a necklace style radio package modified after Amstrup (1980). Nests of radio-marked females were located by following the radio signal (Kenward 1987) and visually observing the female on the nest. Nest site characteristics were measured with a meter stick and included nest width and height, water depth, and height of tallest vegetation (from the ground) within 1 m of the nest, similar to methods described by S. Maxson (unpubl. data).

RESULTS AND DISCUSSION

The nest of a radio-marked American Bittern containing 3 eggs was located on 2 June 1996 in a dense stand of sandbar willow (*Salix exigua*) and giant reed grass. The nest was constructed of residual giant reed grass and measured 29 cm wide and 6 cm tall. The water depth at the nest site was 35 cm and the height of tallest vegetation within 1 m of the nest was 2.25 m (sandbar willow). The female was visually observed incubating the nest on 6 and 7 June but was not flushed; consequently, total number of eggs laid could not be determined. Radio telemetry and visual observation indicated she incubated the eggs until at least 11 June. We discovered at 11:00 CST on 12 June that the nest had been destroyed by a predator. No eggs or egg shells remained in or around the nest. On 8 July, the same radio-marked female was observed incubating a second nest containing 2 eggs. The second nest was located 3 km from the first, was constructed of sedge, and measured 29 cm wide and 4 cm tall. Water depth at the nest site was 35 cm and the height of the tallest vegetation within 1 m of the nest was 1.16 m (sedge). At 10:00 on 17 July, we discovered that a predator had removed one egg from the nest. The radio-marked female was not located at the nest site again. Because of a weak radio transmitter signal, the movements of the radio-marked female following the destruction of the second nest were not known.

These observations confirm the renesting ability of American Bitterns and suggest bitterns possess additional reproductive capability when nests are destroyed by predation or weather related events. This information, along with other life history traits documented by this study (Azure 1998, Brininger 1996), may facilitate further research. Currently, the most effective method of capturing female American Bitterns is to cover them with a dip net when they are on a nest. Renesting American bitterns offer additional opportunities for capture and should be considered when estimating density of nesting females.

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Helping Behavior within Sapsuckers (*Sphyrapicus* spp.)

Cynthia Trombino[1,2]

ABSTRACT.—I documented interspecific and intraspecific helping behavior (more than two adults feeding young at a nest) within sapsuckers of the genus *Sphyrapicus*. Of 120 nests, 97 belonged to Red-breasted (*Sphyrapicus ruber*), Red-naped (*Sphyrapicus nuchalis*), or hybrid (Red-breasted × Red-naped) sapsuckers, and 23 to Williamson's Sapsuckers (*Sphyrapicus thyroideus*). Interspecific helping behavior was observed at two nests (1 with a Red-breasted × Red-naped and hybrid female, 1 with Red-breasted × Red-breasted and Williamson's male) and intraspecific helping behavior (Red-breasted male) was observed at one nest. Given the rarity of helping behavior observed in these species a functional advantage is unlikely; individuals that helped might simply have been responding to a feeding stimulus. *Received 9 Aug. 1999, accepted 23 Dec. 1999.*

Helping occurs when additional birds help the parents care for their offspring (Emlen and Vehrencamp 1983). Intraspecific helping behavior in birds is widespread taxonomically but uncommon, occurring in just 2.4% of bird species (Emlen and Vehrencamp 1983, Stacey and Koenig 1990). In addition to intraspecific helping behavior, interspecific helping behavior has been documented in birds. Taxonomically the distribution of interspecific helping behavior is widespread but rare (reviewed by Shy 1982). In contrast, intraspecific helping behavior occurs frequently in some populations such as Florida Scrub Jays (*Aphelocoma coerulescens*), Acorn Woodpeckers (*Melanerpes formicivorus*), and Red-cockaded Woodpeckers (*Picoides borealis*) (Koenig et al. 1984, Woolfenden and Fitzpatrick 1984, Walters, 1990). In other species, such as Bobolinks (*Dolichonyx oryzivorus*), Brewers Sparrows (*Spizella breweri*), Chipping Sparrows (*Spizella passerina*), and Hooded Warblers (*Wilsonia citrina*), sightings of intraspecific helping occur only rarely (Beason and Trout 1984, Middleton and Prescott 1989, Tarof and Stutchbury 1996, Gill and Krannitz 1997).

It has been suggested that interspecific helping behavior in birds provides evidence that intraspecific helping behavior evolved simply as a consequence of a response to a feeding stimulus (i.e., the begging calls of nestlings; Jamieson and Craig 1987). However, this does not necessarily explain its current functional significance (Ligon and Stacey 1991).

I describe observations of intra- and interspecific helping behavior within the genus *Sphyrapicus*. This genus includes Williamson's Sapsucker (*Sphyrapicus thyroideus*), Red-breasted Sapsucker (*S. ruber*), Red-naped Sapsucker (*S. nuchalis*), and Yellow-bellied Sapsucker (*S. varius*). Rare cases of interspecific helping behavior have been documented between other species in the family Picidae including Hairy Woodpeckers (*Picoides villosus*) feeding Downy Woodpeckers (*Picoides pubescens*), and Three-toed Woodpeckers (*Picoides tridactylus*) feeding Black-backed Woodpeckers (*Picoides arctus*; Davis 1973, Hickery in Shy 1982). This is the first time that helping has been documented between Williamson's and Red-breasted sapsuckers

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and between Red-breasted and Red-naped sapsuckers.

METHODS

The study was conducted in the Fremont National Forest in Lake County, Oregon (42° 30′ N, 120° 40′ W; 1890 m elevation) from March–August, 1994–1996. Study sites included large aspen (*Populus tremuloides*) and willow (*Salix spp.*) meadows and riparian corridors. The surrounding forest is a mixed conifer forest composed largely of lodgepole pine (*Pinus contorta*), ponderosa pine (*Pinus ponderosa*), and white fir (*Abies concolor*). Hybridization between Red-breasted and Red-naped sapsuckers occurs frequently at these sites (Trombino 1998). Williamson's Sapsuckers also nest at these study sites.

Sapsucker nests were located by observing adults feeding young. Red-breasted, Red-naped, and hybrid sapsuckers were color banded when possible by placing mist-nets in flight paths to sapwells or placing insect nets over nest holes while tapping on the tree trunk to encourage the birds to fly out. Unbanded birds could often be identified as Red-breasted, Red-naped, or hybrid by distinct facial plumage characteristics (Trombino 1998). Helping behavior was defined as when more than two adults were seen feeding young.

RESULTS

Ninety-seven Red-breasted, Red-naped, interspecific, and 23 Williamson's Sapsucker nests were located. Interspecific helping occurred at two nests. Interspecific helping behavior was observed at an interspecific nest between 20 June and 10 July 1996. Three sapsuckers were observed feeding young. The first individual was color banded and was classified as a hybrid female based on facial, wing, and tail plumage (Trombino 1998). The second individual was also color banded and was classified as a Red-naped female. The third individual was not color banded but appeared to be a Red-breasted Sapsucker and presumably a male. The nest was observed for 2 hours on 20 June 1996 and on several other occasions until 10 July 1996. Each individual appeared to feed on all occasions and feedings occurred approximately every 4–10 minutes.

Interspecific helping was observed at another nest on 3–5 July 1996. Three sapsuckers were observed feeding young. Two of the individuals were Red-breasted Sapsuckers. The first individual was a color banded female. The second individual was not color banded but appeared to be a male. The third individual was a male Williamson's Sapsucker. The nest was observed for 4 hours on 3 and 5 July. Young were fed 1–11 minutes. All individuals fed young, but the Red-breasted male fed the young less frequently than the other two.

In addition to observations of interspecific helping, intraspecific helping was suspected at one nest. Three Red-breasted Sapsuckers were observed at a nest on 11 July 1996. None of the adults were colored banded but each had a distinct facial pattern. Nestlings were fed at 4–13 minute intervals but feedings did not occur equally between individuals. One of the individuals was seen feeding young on only one occasion and of the remaining two one individual fed the young much more frequently than the other.

DISCUSSION

Helping in Red-breasted and Red-naped sapsuckers occurs infrequently. The best documented cases of helping behavior were interspecific. Helping feed another species' young would seem counter productive. However, in the case of the Red-breasted, hybrid, and Red-naped individuals, extra-pair fertilization cannot be ruled out. In the case of the Red-breasted pair being helped by the Williamson's male it is unlikely that extra pair fertilization had occurred. Hybrids between Red-breasted and Williamson's sapsuckers have not been documented at this site.

It is possible that an unmated male benefits by having the experience of feeding young or by being tolerated in that nesting territory in the following year (Emlen and Vehrencamp 1983). Boundaries of territories shift from year to year and interspecific territoriality occurs between Red-breasted, Red-naped, and Williamson's sapsuckers (unpubl. data). Some cases of helping behavior of other species involved helping by an individual who had lost its mate or had a nest that failed (Shy 1982). This was not documented in the sapsuckers described here but could be a possibility because helping behavior was observed late in the nesting season. Given that helping behavior in sapsuckers occurs rarely, the most likely explanation is that birds are responding strongly to the feeding stimulus (Jamieson and Craig 1987). If there was a functional advantage to helping in sapsuckers, it would be expected to occur more frequently in the population.

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Helping at a Cooper's Hawk Nest

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ABSTRACT.—Nest helping has not been reported previously among Cooper's Hawks (*Accipiter cooperii*). We report a nesting attempt involving three Cooper's Hawks. An adult and subadult male made prey deliveries to an adult female and all three hawks engaged in nest defense. No evidence of intraspecific aggression was observed among the three hawks. *Received 8 Sept. 1999, accepted 8 Dec. 1999.*

Helping is uncommon among breeding Falconiformes (Newton 1979, Skutch 1987). Among North American raptors, helpers have been noted at nests of Mississippi Kites (*Ictinia mississippiensis*; Parker and Ports 1982), Bald Eagles (*Haliaeetus leucocephalus*; Garcelon et al. 1995), Red-tailed Hawks (*Buteo jamaicensis*; Wiley 1975, Santana et al. 1986), Swainson's Hawks (*B. swainsoni*; Cash 1989), American Kestrels (*Falco sparverius*; Wegner 1976), Merlins (*F. columbarius*; James and Oliphant 1986), and the cooperatively breeding Harris' Hawk (*Parabuteo unicinctus*; Mader 1975, Dawson and Mannan 1991). Helping at nests has not been reported for any North American *Accipiter*, but this may be

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due to the difficulty in observing woodland raptors. Here we report observations at a nest that was attended by a female and two male Cooper's Hawks (*Accipiter cooperii*) in Tucson, Arizona.

A possible case of helping in Cooper's Hawks occurred during the 1996 breeding season at a nest discovered 8 April in a small neighborhood park in central Tucson. The pronounced sexual size dimorphism (Snyder and Wiley 1976) and age-specific plumage differences (Rosenfield and Bielefeldt 1993) exhibited by Cooper's Hawks allowed us to visually differentiate between sexes and between adults and subadults. An adult (ASY) female was observed adding sticks to a new nest structure in an aleppo pine (*Pinus halepensis*), and an ASY male made a prey delivery on the day the nest was discovered. The female had an aluminum U.S. Fish & Wildlife Service (USFWS) band on her right leg but the male was unbanded. No other Cooper's Hawks were observed at this time. Presumably the same two ASY Cooper's Hawks were seen again in the nest area on 20 April when another unbanded male made a prey delivery to the banded female. At 11:15 PST on 15 May the female was observed on the nest in an incubation position. The ASY male was not seen but a subadult (SY) male was perched approximately 150 m from the nest tree. The female did not display any discernable attention toward the SY male. During nest checks on 20 and 29 May, the SY male was perched in the nest tree within a few meters of the incubating female. At this time we assumed the SY male had replaced the ASY male. Only the female was observed during nest checks on 4, 10, and 17 June, and two nestlings were observed in the nest.

On 18 June we set a dho-gaza trap (Bloom 1987) with a Great Horned Owl (*Bubo virginianus*) near the nest. Both the ASY female and SY male were present and we captured the female at 05:10 and the male at 05:17. The time between captures was more indicative of the time it took to reset the trap than the aggression level of the SY male. We were processing the two hawks when the *kik* calls (Rosenfield and Bielefeldt 1993) of a male Cooper's Hawk drew our attention to an unbanded ASY male plucking prey atop a nearby telephone pole. We reset the trap and captured the ASY male at 05:45. The band on the female identified her as having been captured in 1995 as a SY bird at a nest 4.4 km away. We banded each male with an aluminum USFWS band and banded all three hawks with alphabetically coded plastic leg bands.

The female, SY male, and both nestlings were seen again on 22 June. On 27 June the banded ASY male was observed bringing prey to the nest area and giving the *kik* vocalization at 05:26. The female flew to the male and perched less than 2 m from him. She did not take the prey but flew to a different location after a few minutes. At 05:35 the SY male flew to the nest area with prey. The female flew to the SY male, took the prey from him, and began eating. Both males left the area shortly thereafter. At no time was there any indication of aggression between any of the Cooper's Hawks. Nestling mortalities from trichomoniasis resulted in nest failure by 30 June and no further observations where made.

There are at least two possible explanations for these observations. First, if our assumption that the SY male replaced the original ASY male is correct, a second ASY male joined the nesting pair. The observation of the female accepting prey from the SY male but not the ASY male suggests the SY male may have held a senior position in the trio. Alternatively, the original ASY male may have been present throughout the breeding season but had simply gone unobserved during several of our nest visits. In the first scenario, only one male is known to have provisioned the female, though the second ASY attempted to do so. In the latter, both males are known to have provisioned the female. In either case, none of the birds displayed any aggression toward each other, and all engaged in nest defense. These behaviors suggest that helping was occurring and are similar to reports in which food provisioning and nest defense were the primary roles among helpers at raptor nests (James and Oliphant 1986, Dawson and Mannan 1991, Garcelon et al. 1995).

Nest helping by related individuals may indirectly increase the helpers' genetic fitness (Woolfenden 1975). We have no information as to the relatedness of the SY and ASY male Cooper's Hawks at the Tucson nest. The ASY female, however, had failed in her nesting attempt the previous year, so we know that she was not the parent of the SY male.

By helping, a male may increase his chances of obtaining copulations with the breeding female (Faaborg et al. 1980). Although Cooper's Hawks are considered monogamous and extra-pair copulations have not been documented for the species (Rosenfield and Bielefeldt 1993), observations by Rosenfield and coworkers (1991) suggest they may occur. However, we did not observe any copulations at the Tucson nest.

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Behavioral Domination of Food Delivery by Tree Swallow Nestlings

Tore Slagsvold[1,3] and Sievert Rohwer[2]

ABSTRACT.—In altricial birds, scramble competition for favorable feeding positions in the nest may cause younger chicks to starve. We studied nestling survival in a population of Tree Swallows (*Tachycineta bicolor*) breeding in nestboxes near Seattle, Washington, in a year of bad weather. Only a mean of 0.5 chicks fledged per nest (range 0–2, 22 nests). Nestling mortality appeared to be caused by starvation. Video filming showed that when chicks were old enough (largest chick within the brood had reached a wing length of about 55–60 mm), they spent much time in the nestbox opening, calling loudly. This behavior seemed to be driven by hunger because it occurred mainly in broods where chicks had low body masses. Parents fed the chick in the opening and did not try to push it back into the nest cavity or go around it. We suspect that blocking of the nestbox opening accelerated mortality of other young in the nest. Such behavior by dominant chicks may be more readily achieved in hole nesting birds with narrow entrances to their nest site than by open nesting birds. *Received 13 Sept. 1999, accepted 10 Feb. 2000.*

In birds, much time elapses between laying the eggs and feeding the chicks. Therefore, many altricial birds are thought to lay a larger clutch than they can typically maintain, and adjust brood size later according to the prevailing food conditions by discrimination against late hatching chicks. Such brood reduction may also be important if all eggs hatch but additional eggs might also serve as insurance in case some eggs fail to hatch (reviewed by Mock and Parker 1997). In some species of birds, brood reduction is proximately caused by siblicide, one chick killing a nest mate. In other species, including most passerines, mortality is caused indirectly by scamble competition for favorable positions in the nest where chicks are most likely to be fed (Lamey and Mock 1991, McRae et al. 1993, Slagsvold 1997). Here we report a study of extreme partial brood loss in Tree Swallows (*Tachycineta bicolor*). These results are important for two reasons. First, nestling mortality was extremely high with only a single chick fledging from most nests in contrast to the usual 3–6 found in this species (Robertson et al. 1992). Second, we present observations of nestling behavior that may provide some insights into the proximate causes of partial brood loss, namely sibling competition.

METHODS

The study was conducted in 1994 in an unsprayed orchard on Whidbey Island (47° 56′ N, 122° 24′ W), north of Seattle, Washington, where wooden nestboxes had been provided since 1985. The 37 mm diameter entrance holes made it difficult for another bird to go around a chick perching in the opening. Six of 13 females with nests we filmed were brownish in color, indicating they were first year birds (Hussell 1983, Robertson et al. 1992). All pairs studied were monogamous as far as we know. Clutch size was 4–6 eggs and most broods hatched within one day.

Parental provisioning was recorded by video filming. A video camera on a tripod was placed 2–3 m from the nestbox. At least two days before filming, one or both parents were trapped using nestbox traps; sexed by plumage color, development of the brood patch, and cloacal protuberance; and individually marked with spots of red, green, or blue Penol marker ink on their breast to help distinguish the sexes. In the 13 nests filmed, hatching occurred between 28 May and 8 July. Nests were filmed for 185–628 min between 10:08 and 20:09 PST (83.3 hours of filming in total for all nests). Each nest was filmed on 1–5 days, 9–22 days after hatching. After each filming bout, we measured the body mass (with a 50 g Pesola spring balance) and wing length (straightened and flattened chord) of all chicks.

RESULTS

Of the 13 nests filmed, two chicks fledged from one nest, one chick fledged from each of

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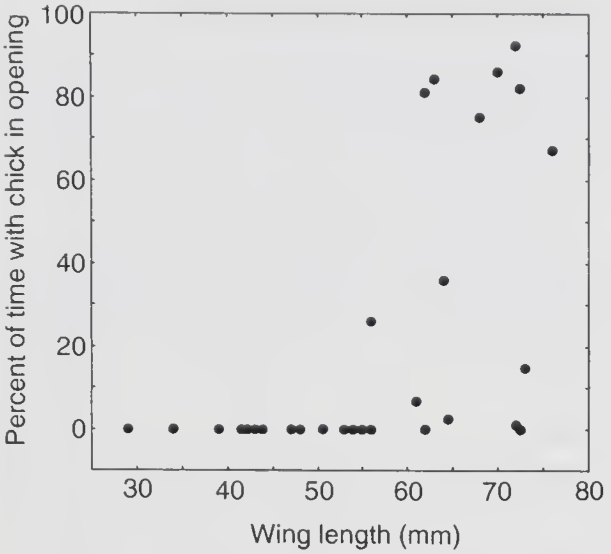

FIG. 1. Percent of time any chick was sitting in the nestbox opening in relation to the wing length of the largest chick within the brood (29 data points from 13 Tree Swallow broods, each filmed 1–5 days).

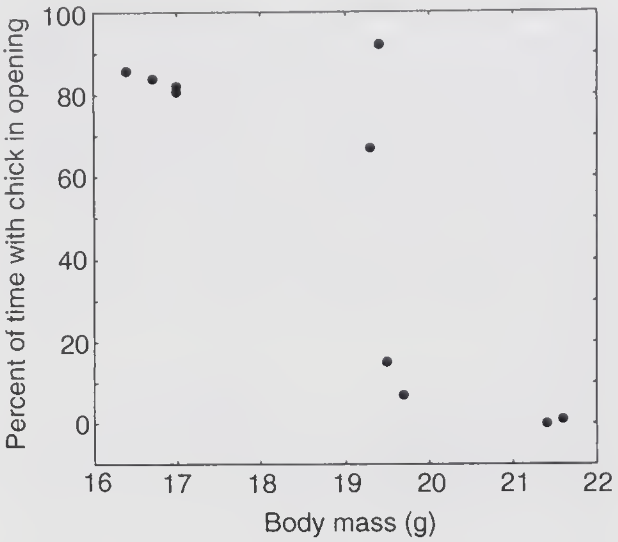

FIG. 2. Percent of time any chick was sitting in the nestbox opening in relation to the body mass of the heaviest chick within the brood.

nine nests, and no chick fledged from three nests (the last and presumably oldest chick died when 13, 14, and 15 days of age in these nests). In 9 additional nests that were not filmed, all chicks had died when the last and presumably oldest chick was 0, 2, 8, 9, 10, 10, 16, 18, and 20 days of age. Hence, mean fledging success for nests in which some chicks hatched was only 0.50 chicks [±0.60 (SD), n = 22]. Eight nests in which some young fledged were filmed both before and after the oldest chick was 16 days old. During filming early in the nestling period the mean brood size at these nests was 2.75 (range 1–4, n = 8); during the late filming all had just a single chick.

Most chicks suffering late mortality were found dead in the nest, apparently having starved. There was no spraying in the orchard nor in the neighborhood. The poor nest success was probably caused by bad weather. Hatching in most nests occurred at the end of May and in the beginning of June. The wind was blowing an average of more than 10 m/sec on 17 days from 1 June to 6 July. There were also many days with rain in June and July (Climatological Data Washington, June, July 1994, National Oceanic and Atmospheric Administration). The combination of wind and rain would have made feeding for an aerial forager very difficult.

High chick mortality suggested that competition for food between chicks was severe, causing chicks to compete for a favorable feeding position. A chick appeared in the nestbox opening when the wing length of the largest chick within the brood was about 55–60 mm (Fig. 1); the chick spent much time there, begging loudly. The chicks were not marked but presumably this chick was the largest and oldest that in most cases occupied this particular position. When the largest chick's wing length was 61–76 mm (body mass 16.4–21.6 g), it occupied the nestbox opening for an average of 52% of the time that it was filmed (Fig. 1; range 0–92%, 10 nests).

We examined the relationship between chick body mass (of the largest chick in case of the only brood with two chicks) and the percent of time any chick was sitting in the nest opening when the largest chicks's wing length was 61–76 mm; the oldest chick was then 16–22 days old. The strongly negative correlation (Spearman rank: $r_s = -0.80$, n = 10, $P = 0.016$; Fig. 2) suggests this behavior was driven by starvation because it occurred mainly in broods where chicks had low body masses. The correlation was also significant if only broods with a single chick was considered ($r_s = -0.75$, $n = 9$, $P = 0.035$). These relationships were not simply due to the age of the chick because there was no significant correlation between the percent of time any chick was sitting in the nest opening and brood age ($r_s = 0.23$, $n = 10$, $P > 0.05$).

Chicks perched in the nestbox opening for long periods even if they were fed, perhaps because they were still hungry (Fig. 2). For instance, one chick (wing length 62 mm) in a nest by itself stayed in the opening continously for 143 min and was fed 27 times by the parents. In another nest with one chick (wing length 72 mm), the chick stayed in the opening continuously for 154 min and was fed 33 times.

Only two nests were filmed that contained more than one chick and where at least one chick spent some time in the nestbox opening. In one case with two chicks (wing length 67 and 68 mm), one chick stayed in the opening continuously for 29 min and was fed 15 times by the parents. Then the sibling stayed in the opening for 10 min and was fed 11 times. Two days later one chick was found dead in the nest and the other chick spent 67% of its time in the nestbox opening. In another case, also with two chicks (wing length 71 and 72 mm recorded two days earlier) one chick stayed in the opening for a maximum of 9 min and was fed three times; both chicks fledged. In both cases, parents fed only the chick in the nestbox opening. The opening was narrow, but the parents never tried to move the chick back into the nest cavity or to move around it if another chick was present inside.

When chicks were 9–15 days old, both parents fed at every nest filmed ($n = 11$). When chicks were 16–22 days old ($n = 10$), the male did not feed at one nest and the female did not feed at another nest.

DISCUSSION

Typically about 80% of Tree Swallow chicks in nestboxes survive and fledge (Robertson et al. 1992). In our study, nestling mortality was extremely high and only an average of 0.5 chicks were produced per nest. The Burke Museum's nest record files contain 10 complete nest histories for Tree Swallows nesting in these very same boxes from 1985 or 1987. These 10 nests fledged an average of 2.0 young with 7 nests that fledged young producing an average of 2.9 young. Thus, 1994 seems to have been an unusually bad year for Tree Swallows nesting at this locality. The poor nest success was probably caused by long periods of windy and rainy weather during the nestling stage. The body mass of well-fed Tree Swallow nestlings peaks at 22–24 g on days 12–14, followed by a recession until fledging at the adult weight of 20–21 g (Zach and Mayoh 1982, Robertson et al. 1992). In our study, body masses were generally much lower than those values (Fig. 2).

In altricial birds, siblings compete for favorable positions in the nest; in hole-nesters this should be at the nest hole (Gottlander 1987, Kacelnik et al. 1995, Leonard and Horn 1996). An extreme form of competition seemed to occur in our study of the population of Tree Swallows because one chick sometimes occupied the nestbox opening for hours. Nesting in a cavity with a narrow entrance hole may facilitate monopolization of parental care because the parents did not attempt to go around the chick blocking the entrance hole. When food is plentiful, chicks may frequently shift positions in the nest in relation to their needs, allowing food to be more evenly distributed across the brood (Reed 1981, Haftorn 1986). In our study, a chick did not necessarily move back after being fed, presumably because it was still hungry. Perching at the nest entrance mainly occurred in broods where chicks had low body masses, suggesting that the behavior is costly and conditional. Perching chicks may be more accessible to predators and they may be more readily detected, in particular if calling (Haskell 1994).

Hatching of the brood was relatively synchronous but this does not mean that all chicks suffered equally. If all chicks are starving but one is able to occupy the nest entrance over some period of time, then that chick may soon gain an advantage because it would be the only one to be fed during that period and so the only one to add resources for fighting and growth. Hence, we suggest that starvation was ultimately caused by bad weather and poor feeding conditions, but that nest hole blocking by dominant chicks may have accelerated mortality of nest mates in some nests.

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An Instance of Helping Behavior in Northern Rough-winged Swallows

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ABSTRACT.—During June 1999, in Grand Isle, Vermont, four Northern Rough-winged Swallows (*Stelgidopteryx serripennis*) fed five nestlings at one nest. A second nest 3 m away had been depredated. The four swallows continued their unusual cooperative behavior until the young had fledged. *Received 1 Oct. 1999, accepted 26 Jan. 2000.*

Northern Rough-winged Swallows (*Stelgidopteryx serripennis*) have expanded their breeding range northward in recent years (Norse 1985, Levine 1988). I first observed them in Grand Isle, Vermont on Lake Champlain in April 1988. Grand Isle nest sites include the hollow bricks of a barn wall and the eaves of a porch roof. Typical nest locations are the natural cavities and Belted Kingfisher (*Ceryle alcyon*) burrows along the shoreline.

At 16:00 EST on 9 June 1999, I searched for nests of Northern Rough-winged Swallows at one of their traditional breeding locales, a cove on the shore of Grand Isle (44° 43′ N, 73° 21′ W). Five or six adults swooped at and scolded me as I inspected nests in the drainage tiles of a concrete seawall. Tile 1 (Nest 1) contained five newly hatched young. Three meters beyond Tile 1, Tile 2 (Nest 2) contained two intact eggs, one or two partially hatched eggs, and one or two hatchlings. The nests were 25–30 cm inside the entrance of each 10 cm diameter tile. The tiles were situated 1 m from the top of the southwest facing wall and 2.5 m above the lake. Two previously used sites, Tile 3 (Nest 3) and a small rock cleft (Nest 4) 14 m beyond Tile 3, were unoccupied.

I observed the cove for 30 minutes on 20 June with 10 × 50 binoculars and 30 × 122 spotting scope. Six adult Northern Rough-

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winged Swallows foraged in the cove. Prey items were abundant and included mayflies (*Hexagenia* spp.). Consequently, foraging trips were short. With all six swallows in the field of view for extended periods of time, I determined that four of the six swallows were, in quick succession, visiting Tile 1. As soon as one of the four swallows exited Tile 1, the next in line would enter. During the 30 minute observation, I saw no agonistic behavior among the four swallows as they continually entered and exited Tile 1. These four swallows did not intermingle with the other two swallows, thus facilitating the tracking of each swallow. Because Tile 1 was 150 m away, I could not determine whether each adult delivered prey items to the nestlings within the tile; however, I observed the adults removing fecal sacs. At the conclusion of their feeding activity, the four adults perched together on the bare branches of a fallen tree.

The other two Northern Rough-winged Swallows carried food to a second nest (Nest 5) within the shale ledge 2 m from Nest 4. Nest 5 contained five nestlings similar in size to the five nestlings in Tile 1.

No swallows visited the abandoned nest in Tile 2, which contained half an eggshell only. Because Northern Rough-winged Swallows remove eggshells from their nests during hatching (Dejong 1996), depredation of Tile 2 is assumed to have occurred 9 or 10 June. Embedded in the concrete at the entrance of the depredated nest was a metal reinforcing strap, a perch that might have allowed easy access by a predator. Unoccupied Tile 3 also had a metal strap at the entrance. In contrast, Tile 1 with a successful nest had no such perch.

At 13:00 on 27 June, six adult Northern Rough-winged Swallows still foraged in the cove. As before, four swallows entered Tile 1 and two entered Nest 5. Two more adult swallows soon joined the six scolding adults while I was inspecting Tile 1. Another active Northern Rough-winged Swallow nest (Nest 6) existed less than 1 km north of the cove.

When I checked the cove at various times 29–30 June, I observed either four or six adult Northern Rough-winged Swallows. The young swallows in Tile 1 fledged 1 July and left the cove. After 12:30, I observed only two swallows foraging over the cove. The young swallows in Nest 5 fledged 2 July and remained in the area in association with two adults through 3 July.

Dejong (1996) noted that cooperative breeding of Northern Rough-winged Swallows had not been observed. Robertson and coworkers (1992) suggested that "investigatory visits" (sporadic visits that often involve attempted theft of food) may be misinterpreted as cooperative breeding. The continued presence of four adult Northern Rough-winged Swallows engaged in apparent feeding activity at one nest, following the loss of an adjacent nest, suggests shared parental activity. Perhaps the pair of swallows that lost their nestlings readily adopted nestlings of similar age 3 m from the pair's own nest. This was an isolated example of helping behavior that was unlikely to provide any evolutionary advantage (see Lombardo 1986 for discussion).

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Tool Modification and Use by an American Crow

Carolee Caffrey[1]

ABSTRACT—An American Crow (*Corvus brachyrhynchos*) was observed to modify and use a piece of wood as a probe. *Received 21 Oct., 1999, accepted 19 Feb. 2000.*

The use of tools has been described in many species of birds, including several corvids (Jones and Kamil 1973; Boswall 1977, 1978, 1983a, 1983b; Beck 1980). Members of a few species of the genus *Corvus* are known to use, and even manufacture, tools (Montevecchi 1978, Hunt 1996), yet such behavior has not been reported for other species. Here, I describe a recent observation of tool modification and use in American Crows (*Corvus brachyrhynchos*).

As part of a study on American Crows in Stillwater, Oklahoma, I marked individuals with patagial tags and colored leg bands. On 21 September 1999, while observing three members of a family of five crows foraging in a residential area, I saw the lone unmarked individual walk along a wooden fence railing to the end post. With its bill, it attempted to probe the interior of the hole supporting the railing but the space was too small for the bird to penetrate very far. The crow then pecked at the wood surrounding the hole and loosened a section at the top, which it pulled until a triangular piece broke off. It took the piece of wood and placed it under its feet, with the

FIG. 1. The tool used by an American Crow.

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wide end closest to its body, and hammered several times at the tapered end. It then picked up the piece of wood by the wide end and probed the hole with the pointed end for approximately 20 seconds. The female breeder, who had just left the area, called from a tree about 200 meters away and the individual probing the hole stopped and looked toward her. It turned and placed the tool into the hole and flew to join the female. I went to the hole, saw only the remains of a spider's web inside, and retrieved the piece of wood (Fig. 1). It did not match exactly the gap from which it had been pulled; the tapered end had been narrowed. A few days later, when I approached the post, a large spider dashed out of the hole and disappeared.

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First Description of Nest and Nesting Behavior of the Nightingale Wren

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ABSTRACT.—Nests and nesting behavior of the Nightingale Wren (*Microcerculus marginatus*) in Panama are described. Two nests were found at the ends of horizontal burrows in dirt banks, presumably excavated by other species. The nest chambers were lined with dead leaf fragments. Clutch sizes were two and three eggs. Incubation period was 19 or 20 days for one nest, and the nestling period was 16 or 17 days for the second nest. A comparison of nests in the Troglodytidae shows the nests of *M. marginatus* to be most similar to those of the genera *Salpinctes*, *Catherpes*, and *Hylorchilus*, all of which are secondary cavity nesters. If nest type is a phylogenetically conserved characteristic, then these four genera may be more closely related than is reflected in current classifications. *Received 29 June 1999, accepted 13 Nov. 1999.*

The Nightingale Wren (*Microcerculus marginatus*; A.O.U. 1998; Troglodytidae) is a terrestrial resident of humid forest undergrowth from Costa Rica south to Bolivia and Brazil (Stiles 1983, Ridgely and Tudor 1997). The vocalizations and plumages of *M. marginatus* have been described (Slud 1958, Stiles 1983, Hardy and Delaney 1987); however, its nest and nesting behavior are unknown. Hilty and Brown (1986) noted a bird "nest building" on 15 February in the upper Anchicayá Valley of Colombia, but we could find nothing they published about the nest. Schönwetter (1979) described one repaired egg from Venezuela as white, but mentioned nothing about the nest or nesting behavior. Lack of information on the nests and nesting behavior of tropical birds hinders comparative studies and development of conservation plans. Here we describe the first known nests of the species and nesting

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behavior of two pairs of *M. m. luscinia* from the Republic of Panama.

NEST SITE AND METHODS

The first nest (nest A) was found at the Parque Nacional Soberanía (9° 05′ N, 79° 40′ W, 90 m elevation), 3 km southeast of the junction of the Río Chagres and the Panama Canal. The vegetation of the area is mature, lowland tropical humid forest with low hills cut by steep ravines. The second nest (nest B) was found 4 km north of Santa Clara, Chiriquí province (8° 51′ N, 82° 43′ W), at 1600 m elevation in mature montane forest with a canopy height of 35 m. Both nests were found during random nest searching by unintentionally flushing the birds from the nest hole. Nest A was monitored once every 2–3 days and nest B was monitored almost daily. At nest A nestling development was recorded with the aid of a flashlight and mirror. One adult was banded at nest B, but because of difficulty in seeing the birds, we could not determine whether both adults were involved in incubation or feeding bouts. The nests were observed from 10 m with 10 × 42 binoculars.

RESULTS AND DISCUSSION

Nest placement and description.—Both nests of *M. marginatus* were at the distal end of horizontal burrows in earthen banks and lined with a mat of dead leaves. The immediate area around both nest holes was bare earth with nothing concealing the entrance holes. We suspect nest A was an old nest burrow of a Scaly-throated Leaftosser (*Sclerurus guatemalensis*) and that nest B was an old nest burrow of a Blue-crowned Motmot (*Momotus momota*), because of the similar structure to nearby burrows known to be excavated by these species.

Nest A was found on 8 July 1996 during the incubation phase. The area around nest A had a sparsely vegetated understory and ground cover. It was about 50 cm up on the side of a steep (ca 75°) earthen bank bordering a small stream. The dimensions of the entrance tunnel were about 9 cm deep, 3.9 cm high, and 7.1 cm wide. The diameter of the spherical nesting chamber was 11 cm.

On 13 May 1997 we located nest B during nest building. The area near nest B had a dense understory of shrubs, ferns, and herbaceous plants. Nest B was 61 cm from the bottom and 35 cm from the top of a vertical earthen bank created by a road cut. The dimensions of the entrance tunnel were about 50 cm deep, 8.0 cm high, and 10.6 cm wide. The nest chamber of nest B was inaccessible and therefore not measured.

Nest building behavior.—About a week before initiating their clutch, we observed pair B building their nest for 125 min. They made 24.5 trips/h, during which they brought single dead-leaf fragments to the nest. Only twice was a bird seen carrying more than one leaf fragment at a time. The adult(s) averaged 25 s inside the nest (range 15–35 s). The adult(s) were seen nest building on two days after the nest was found, but it is unknown how long they spent building before discovery. At no point was an adult seen excavating the nest hole.

Clutch and brood size.—The clutch and brood size for nest A was three and for nest B was two. The eggs of both nests were white and unmarked. Because of difficulties in observing the eggs, the shape and measurements were undetermined.

Incubation.—In 105 min of observation at nest A, one member of the pair was on the nest for 83 min consecutively and left it unattended for 22 min. At nest B, in four observations of 120 min each, the total time one or both adults were in the burrow averaged 92.5 min [±10.3 min (SD)], and the total time away from the nest averaged 28.0 min (±6.9 min). We were unable to check the nest during the week of laying and early incubation. The first day of incubation for nest B was estimated by tracking the duration of time the adult(s) remained in the nest after nest building was over. The incubation period, as measured from the first day of adult incubation behavior (21 or 22 May) until hatching on 9 June, was 19 or 20 days.

Feeding of nestlings.—Hatching synchrony for nest A was undetermined. We made 3 observations of 60 min each at nest A, when the nestlings were 13–16 days old; the adult(s) visited the nest at a rate of 5.6 times/h with food and removed 1–2 fecal sacs at a rate of 1.3 times/h. In the 1 h periods the adults' total time outside the nest averaged 58.7 min (±0.35 min), and total time inside the nest averaged 1.3 min (±0.35 min). Spiders (n = 3) and orthopterans (n = 1) were brought to the nest; however, most prey items could not be identified. Only one adult was seen entering the nest at a time. The nestling period for nest A was from 20 or 21 July to 5 August, 16 or 17 days.

The nest B nestlings hatched on the same day. Nest B was observed on four days for 60 min each when the nestlings were 2, 3, 4, and 5 days of age. In these 1 h periods the adult(s) fed the nestlings at a rate of 2 visits/h. Their total time inside the nest averaged 37.0 min (±10.7 min) and total time outside the nest averaged 23.0 min (±10.7 min).

Nestling development.—Nestlings at nest A, at 1–2 days of age, were pink and covered with gray down. By days 6–7, they retained gray down on their heads and backs and they had pin feathers on the capital and spinal tracts. By days 9–10, pin feathers on the alar tract were well developed, and broken sheaths exposed tips of rufous-brown feathers on the spinal tracts. The fleshy parts of the bills were gray-dusky and the eyes were not completely open. By days 11–12, the eyes were fully open and many broken feather sheaths exposed rufous-brown feathers on the spinal tract. One nestling appeared smaller than the others, possibly having hatched later. By days 13–14, the distal two thirds of the bill was dark brown, and the proximal portion was gray-dusky. The fully developed back feathers were dark brown, and the upper breast feathers were gray with slate bars. Pin feathers dominated the capital tract and broken sheaths exposed white feathers on the throat. By days 15–16 the nestlings appeared fully feathered and had dark brown feathers, edged with slate, covering the crowns.

Nest fate.—On 5 August 1996 all three nestlings from nest A successfully fledged. On 16 June 1997 nest B was found with one dead and putrid 6–8 day old nestling, halfway down the tunnel, with a hole in its back. The other nestling was gone.

Systematic implications.—Nest type has often been used to infer systematic relationships within bird families (Vaurie 1980). Winkler and Sheldon (1993) demonstrated a strong link between nest type and phylogeny in the Hirundinidae. *Microcerculus marginatus* is the only burrow-nesting species known in the family Troglodytidae whose members mostly have enclosed, retort-shaped nests (Wetmore et al. 1984, Hilty and Brown 1986, Stiles and Skutch 1989, Sick 1993, Howell and Webb 1995, Baicich and Harrison 1997).

Availability of earthen burrows and competition for other kinds of crevices may explain the use of earthen burrows by *M. marginatus.* Earthen burrows were commonly excavated by several species in the humid forest where we worked and many were abandoned by their primary owners. Rocky crevices seemed to be virtually nonexistant. Other types of cavities may have been unavailable to the wrens because of competition with several other species of secondary cavity users, location in a different strata of the forest, or both. In the Troglodytidae, the Rock Wren (*Salpinctes obsoletus*), the Canyon Wren (*Catherpes mexicanus*), and the Sumichrast's Wren (*Hylorchilus sumichrasti*), which mainly build cup nests inside cavities, have the most similar nest types to *M. marginatus* (Stiles and Skutch 1989, Howell and Webb 1995, Baicich and Harrison 1997). The other wrens in the family that occasionally nest in cavities (*Troglodytes* spp., *Thryomanes bewickii, Thryothorus ludovicianus*) construct domed type nests rather than a simple cup (Stiles and Skutch 1989, Howell and Webb 1995, Baicich and Harrison 1997).

Traditional classifications place *Microcerculus* far from *Catherpes, Salpinctes,* and *Hylorchilus* (e.g., Peters 1960, A.O.U. 1998). If nest type is a conserved phylogenetic character, then it is possible that the common use of cavities and burrows and the construction of a simple nest cup (non-domed) in these genera may support a closer phylogenetic relationship than is reflected currently. Alternatively the shared nest type may be convergence caused by similarities in the niches they occupy.

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An Observation of Cooperative Breeding in the Ovenbird

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ABSTRACT.—During June and July, 1999, we observed two male Ovenbirds (*Seiurus aurocapillus*) caring for recently fledged Ovenbird chicks from the same nest in what we believe was the outcome of a polyandrous relationship. If so, the circumstances surrounding this observation are similar to the only other published account of polyandry in this species. We suggest that the reason for the adoption of this behavior may be related to a shortage of females. If this is the case, then polyandry may be more widespread in Ovenbirds than previously thought because we regularly observed unmated male Ovenbirds on our study plots, indicating that the conditions favoring polyandry (limited access to females) occur relatively frequently.

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Polyandry describes a mating system in which one female mates with two or more males, and these males are each mated to only one female (Oring 1982, 1986). Polyandry has been reported in only 1% of all bird species and is largely restricted to shorebirds (Oring 1982, 1986). However, polyandry has been reported in a few passerines, including the Ovenbird (*Seiurus aurocapillus*; Hann 1940). In this paper, we report an observation of cooperative breeding by two male Ovenbirds that we believe represents an additional case of polyandrous mating in this species.

The observation took place on the Bartlett Experimental Forest in Carroll Co., New Hampshire (44° 04′ N, 71° 17′ W). On 12 May, 1999 a male Ovenbird was captured and color banded Y/RA. On 21 May, we located a nest, which was depredated during the nestling stage on 7 June. It was clear that this nest belonged to Y/RA; he was seen escorting the female as she built it and he exclusively sang above the nest. Another male was captured on the territory to the south on 21 May and banded O/OA. Based on several lines of evidence, we concluded that O/OA was unmated during the period between the capture of Y/RA and the depredation of Y/RA's nest; we never saw O/OA with a female during several weeks of observation, we never found a nest on his territory, and he sang steadily from high in the canopy in a manner commonly ob-

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served in unmated male Ovenbirds (D.I.K., pers. obs.). Three days after Y/RA's nest was depredated, a nearly completed empty Ovenbird nest was located 20 m south of Y/RA's first nest. Although Y/RA was observed copulating with an unbanded female near the new nest on at least one occasion, we concluded that this nest belonged to O/OA because he was seen singing over the new nest and escorting an unbanded female back to the nest after bouts of nest building or incubation. Furthermore, Y/RA shifted his singing activity about 70 m northwest after his nest was depredated. Although he occasionally sang from a perch close to the site of the nest that was depredated on 7 June, he never sang over the new nest. Except when he was seen copulating with a female at O/OA's nest, Y/RA was never seen with a female after his nest was depredated during weeks of intensive observation; we never found another nest on his territory. On 6 July, we banded the nestlings in O/OA's nest and they did not return to the nest. Three of the nestlings remained near (<30 m) the nest and were fed by O/OA and an unbanded female. A fourth nestling was escorted to the north by Y/RA and, on 7 July, was located being fed by Y/RA 270 m north of the nest.

Because the female on O/OA's territory and the female seen copulating with Y/RA near O/OA's nest were unbanded, we are unable to conclude with certainty that these observations were of the same female. However, circumstantial evidence suggests that the female occupying O/OA's territory and the female seen copulating with Y/R/A were the same. First, O/OA's acquisition of a mate coincided with the onset of a period during which Y/RA was unmated. Second, three experienced observers failed to detect a female on Y/RA's territory after the loss of his first nest during repeated visits throughout the following months. Third, the females in all of the surrounding territories were incubating; thus, they were not receptive and would not be expected to solicit copulations from neighboring males. Fourth, the nearest nest from which a female could have approached was more than 100 m distant. On the basis of this evidence, we strongly suspect that our observations represent a case of polyandry. In the only published account of polyandry in the Ovenbird, two males occupying adjacent territories fed young in the same nest and divided the brood up among themselves, each took chicks back to his respective territory after fledging (Hann 1940). Our observation is similar except that we do not know if both males fed the young while they were in the nest.

Our observation is not consistent with pseudopolyandry in which extra males merely help to feed the young (Mayr 1939) because the female in this case both occupied O/OA's territory and evidently copulated with Y/RA. Rather, our observation and that of Hann (1940) correspond to an uncommon form of polyandry referred to by Oring (1982, 1986) as "cooperative simultaneous polyandry", in which more than one male is mated with one female and the single clutch of mixed parentage is reared cooperatively by the female and her several mates. Reasons proposed for the adoption of this form of reproduction include restricted access to resources necessary for breeding, such as suitable habitat or mates (Brown 1987). There appears to be abundant unoccupied habitat of suitable quality in our study area. It is possible that the availability of females is limited. Consistent with this idea is our observation that O/OA remained unmated for a prolonged period early in the season, the high proportion of unmated males (ca 50%) on a separate study plot nearby, and the presence of unmated Ovenbird males reported in previous studies in this region (King et al. 1996). The regularly restricted availability of females suggest that the frequency of this type of mating behavior might be more frequent than previously believed (Hann 1940).

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Nocturnal Singing in Grassland Birds

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ABSTRACT.—We conducted unlimited radius point counts from March–July 1999 at sunrise, dusk, and night to document the relative frequency of nocturnal singing by grassland birds at Prairie Ridge State Natural Area, Jasper County, Illinois. Most grassland species were recorded singing at all times of day, but least commonly at night. Short-eared Owls (*Asio flammeus*) and American Woodcock (*Scolopax minor*) were only recorded at dusk and night. Sedge Wrens (*Cistothorus platensis*) and Henslow's Sparrows (*Ammodramus henslowii*) were most frequently recorded at night and least frequently at sunrise. Only 57% of all the breeding species recorded by our surveys were detected on June sunrise counts corresponding to the timing of the North American Breeding Bird Survey. *Received 15 Sept. 1999, accepted 9 Feb. 2000.*

Nocturnal singing is well documented for some diurnal avian species, such as the Northern Mockingbird (*Mimus polyglottos*; Derrickson and Brietwisch 1992) and Marsh Wren (*Cistothorus palustris*; Barclay et al. 1985). Several grassland *Ammodramus* sparrow species are known to occasionally sing at night (Smith 1992, Rising 1996, Vickery 1996), although Smith (1992:316) noted "observers may have exaggerated the frequency of this behavior by Henslow's Sparrows (*A. henslowii*)." Gross (1968) heard Dickcissels (*Spiza americana*) calling at dusk but not at night. Nighttime singing has been noted for the Western Meadowlark (*Sturnella neglecta*), but apparently has not been recorded for the Eastern Meadowlark (*S. magna*; Lanyon 1957, 1995). To document nocturnal singing and to quantify this behavior relative to singing at other times of the day, we conducted surveys at sunrise, dusk, and night throughout the 1999 breeding season on a grassland reserve in southeastern Illinois.

METHODS

We conducted our surveys at Prairie Ridge State Natural Area (SNA), Jasper County, Illinois (38° 55′ N, 88° 12′ W). Prairie Ridge SNA consists of 635 ha of restored grasslands managed by the Illinois Department of Natural Resources for threatened and endangered wildlife [see Walk and Warner (1999) for a more detailed description of vegetation and management]. The surrounding landscape is approximately 72% corn (*Zea mays*) and soybean (*Glycine max*) rowcrop agriculture, 12% wheat (*Triticum aestivum*), and small areas of pasture, woodland, roads, farmsteads, and other land uses.

We established 13 roadside points adjacent to grasslands and at least 1 km apart. During the first half of each month from March through July 1999, we conducted a 4-min, unlimited-radius count from each point at three time periods/day: sunrise, dusk, and night. Sunrise surveys began at local sunrise, dusk surveys began 0.5 hour after local sunset, and night surveys began 4.0 hours after sunset. Points were always surveyed in the same sequence and all points required approximately 1.5 hours to complete. Because nocturnal singing may be strongly influenced by ambient light levels and weather conditions (Shaver and Walker 1930, Gibbs and Melvin 1993), we conducted these counts only when cloud cover was less than 5% and wind speeds were less than 10 km/hour. The phase of the moon was recorded for count periods when it was visible. However, our counts were too infrequent to thoroughly evaluate the effects of moonlight on nocturnal singing. Because our objective was to quantify the occurrence of nocturnal singing, only primary songs or displays were recorded; birds that were visually detected were not considered. Flight, alarm, or call notes (when separable from primary song) were excluded. Species recorded were confirmed to be breeding on the study site by nest locations or observations of dependent young during other avian studies (Kershner and Walk, unpubl. data).

RESULTS

In 195 point counts, we recorded 49 breeding species. The seasonal and daily patterns of recording 20 grassland-nesting species are given in Table 1. The Short-eared Owl (*Asio flammeus*) and American Woodcock (*Scolopax minor*) were recorded only at dusk or night whereas all other grassland species were

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TABLE 1. Seasons and times of day (S = sunrise; D = dusk; N = night) that grassland nesting species were heard singing in 1999, Jasper County, Illinois.

Species	March	April	May	June	July
American Bittern			S D N		
Mallard	S D N	S D N			
Ring-necked Pheasant		S	S	S	S
Greater Prairie-Chicken		S D	S	S	S
Northern Bobwhite		S	S	S	S
Killdeer	S D N	S D N	S D N	S D N	S D N
Upland Sandpiper			S		S
American Woodcock	D N	N	D N		
Short-eared Owl	D N				
Loggerhead Shrike	S		S		
Horned Lark	S	S D N	S D	S	
Sedge Wren			D	N	S D N
Common Yellowthroat			S D	S	S
Field Sparrow		S	S N	S N	S
Grasshopper Sparrow			S D	S	S
Henslow's Sparrow			S D N	D N	S D N
Dickcissel			S D	S D	S N
Red-winged Blackbird	S	S	S D	S D	S
Eastern Meadowlark	S	S D N	S D	S	S
American Goldfinch			S	S	S

recorded during sunrise surveys. The number of species recorded within each month was greatest at sunrise, with fewer species noted at dusk and night (Table 1).

Eight species were recorded frequently enough to compare singing patterns among time periods (Table 2). Collectively, Eastern Meadowlarks, Red-winged Blackbirds (*Agelaius phoeniceus*), Dickcissels, Field Sparrows (*Spizella pusilla*), and Horned Larks (*Eremophila alpestris*) were heard mostly at sunrise. At times other than our point counts, we noted each of these species occasionally singing throughout the night during the 1999 breeding season. Killdeer were detected less at dusk than sunrise or night (Table 2).

Henslow's Sparrows and Sedge Wrens (*Cistothorus platensis*) were recorded more frequently at night than at sunrise (Table 2). Both species were only recorded during the point counts conducted in May, June, and July. A mean of 1.44 Henslow's Sparrows/point was recorded at night, significantly more than the mean of 0.38 sparrows/point recorded at sunrise (paired t-statistic = 4.09, $P < 0.001$, 38 df). Numbers of Henslow's Sparrows ob-

TABLE 2. Mean number of birds recorded per point count at sunrise, dusk, and night in 1999, Jasper County, Illinois. Only counts during months in which a species was recorded were considered. Values within species marked with differing superscripts are significantly different ($P < 0.05$). Species are listed from most diurnally to most nocturnally recorded.

	Mean birds/point (SE)		
Species	Sunrise	Dusk	Night
Red-winged blackbird	9.55 (0.83)^{A}	0.23 (0.14)^{B}	not recorded
Eastern Meadowlark	4.65 (0.37)^{A}	0.06 (0.05)^{B}	0.02 (0.02)^{B}
Dickcissel	3.33 (0.40)^{A}	0.15 (0.09)^{B}	0.03 (0.03)^{B}
Horned Lark	1.75 (0.27)^{A}	0.17 (0.12)^{B}	0.02 (0.02)^{B}
Field Sparrow	1.08 (0.22)^{A}	not recorded	0.08 (0.04)^{B}
Killdeer	1.57 (0.16)^{A}	1.00 (0.17)^{B}	1.78 (0.27)^{A}
Sedge Wren	0.13 (0.11)^{A}	0.15 (0.07)^{A}	0.49 (0.19)^{B}
Henslow's Sparrow	0.38 (0.15)^{A}	0.56 (0.19)^{A}	1.44 (0.30)^{B}

served at dusk were intermediate (0.56 birds/point). Similar numbers of Sedge Wrens were heard at sunrise and dusk (0.13 and 0.15 wrens/point, respectively), versus greater numbers at night (0.49 wrens/point) compared to sunrise (paired *t*-statistic = 2.41, P = 0.021, 38 df).

DISCUSSION

Sedge Wrens and Henslow's Sparrows were detected more frequently at night than other times of day. Recordings of greater numbers of these species at night than sunrise was probably related to reduced song interference at night; both species could be detected at longer distances when fewer other birds were vocal. For this reason, Barclay and coworkers (1985) hypothesized that nocturnal singing in Marsh Wrens serves to facilitate male-male vocal interactions. Walkinshaw (1935) noted that male Sedge Wrens sang as persistently at night as during daylight hours.

Killdeer, American Woodcock, and Henslow's Sparrows tended to be especially vocal on moonlit nights. Species also appeared more likely to sing at dusk or night at the onset of their breeding season (see Fisler 1962; see Walk et al. 1999 for local nesting dates of most grassland birds); Eastern Meadowlarks and Horned Larks were heard at dusk and night primarily in April, and Greater Prairie-Chickens (*Tympanuchus cupido*) only displayed at dusk in April.

In addition to showing the need for night surveys to record crepuscular and nocturnal species and the potential to achieve better population estimates for Henslow's Sparrows and Sedge Wrens, our results reveal the inadequacy of single period sunrise surveys to record all breeding species. Protocols similar to the North American Breeding Bird Survey protocol, using early-morning June counts, might fail to detect many breeding species. We heard only 57% of the breeding species on our June sunrise point counts. None of the species recorded only in other months or at other times of day was visually noted on our June sunrise point counts. Counts at other times of year have faults, including breeding inactivity by many species and an indeterminable proportion of migrant birds. Furthermore, night songs sometimes differ qualitatively from day songs (Barclay et al. 1985, Lougheed and Handford 1989), bringing into question the function of night songs and the gender and territorial status of night singers. Multiple surveys are necessary to monitor all breeding species at a given location, and the bias of single-period surveys needs to be considered in these census data.

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Predation on Birds Caught in Mist-Nets in Upland Kenyan Forest Fragments

Thomas Brooks[1,2]

ABSTRACT.—I report a predation rate of 24 birds from 3707 total captures of birds caught in mist-nets in fragmented upland forests in Kenya. Predation was highly concentrated in specific forest fragments, with multiple birds simultaneously found killed in more than half of the predation events. Predators were probably attracted to the mist-nets by the noise and activity of the netted birds because the capture rate of predated nets was more than three times the mean for the survey as a whole. The most common victims were Yellow-whiskered Greenbuls (*Andropadus latirostris*), and the most common predators were blue monkeys (*Cercopithecus mitis*). Although 20% of all our mist-net captures were in Kakamega, a large forest, not a single bird was taken from our nets there, suggesting that predation rates on mist-netted birds are higher in small forest fragments. *Received 5 May 1999, accepted 22 Dec. 1999.*

Throughout 1996, we surveyed birds in three fragmented upland Kenyan forests (Brooks and Waiyaki 1996) as part of an assessment of the time-lag between deforestation and local extinction of forest birds (Brooks et al. 1999). The three forests were Kakamega (1400–1600 m; April–May and September), the Taita Hills (1500–1800 m; July–August) and the southwestern flank of Mt. Kenya (2000–2100 m; October–November). These surveys involved a large amount of mist-netting, which we will summarize elsewhere. The purpose of this note is to report on some incidents of predation on birds caught in the mist-nets.

Throughout our fieldwork, we deliberately minimized the incidence of predation on mist-netted birds by checking nets regularly (normally with a maximum of 1 hr between net-rounds) and actively scaring away predators, particularly blue monkeys (*Cercopithecus mitis*), when they were seen near the nets. All nets were about 20 m long and had four panels (ca 2 m high); we opened all nets at dawn, closed them during rain, and closed and furled them overnight. We operated a total of 300 net-hours in all large forest fragments (five in each forest) with two consecutive lines of 10 nets run perpendicular to the forest edge into the interior for 15 hours each. For each of these 200 m net-lines, we operated nets for one full day and early the following morning. In the main Kakamega Forest, we also ran 300 net-hours in this fashion in one subplot and 80 net-hours (as one line of 10 nets run for 4 hours from dawn on each of two mornings) in eight additional subplots (Oyugi 1998). For sites too small to accommodate 400 m of mist-net (three patches in the Taita Hills and four on Mount Kenya), we ran a single line of 5 nets for one day (50 net-hours each location).

In total, we caught 3091 individual birds,

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TABLE 1. Predation on birds caught in mist-nets in three upland forests in Kenya. Species of prey is followed by species (or likely species) of predator and number of predation incidents at that site. Systematic order of bird species in each site follows Zimmerman et al. (1996).

Site	Bird species	Predator species	*n*
KAKAMEGA			
Ikuywa	*Andropadus latirostris*	small mammal	2
		Cercopithecus mitis	2
	unidentified	*Cercopithecus mitis*	6
Malava West	*Phyllastrephus cabanisi*	*Accipiter tachiro*	1
TAITA HILLS			
Chawia	*Nectarinia olivacea*	unidentified	1
Mbololo	*Pogonocichla stellata*	safari ants	1
MT KENYA			
Chehe	*Pogonocichla stellata*	unidentified	1
	Nectarinia olivacea	*Accipiter tachiro*	1
Ragati	*Andropadus latirostris*	*Cercopithecus mitis*	1
	Andropadus nigriceps	*Cercopithecus mitis*	1
	Bradypterus lopezi	*Cercopithecus mitis*	1
Muthira	*Andropadus latirostris*	*Cercopithecus mitis*	3
	Trochocercus albonotatus	*Cercopithecus mitis*	1
	Malaconotus nigrifrons	*Cercopithecus mitis*	1
	Mandingoa nitidula	*Cercopithecus mitis*	1

of which 24 (0.8%) were predated (Table 1). The overall predation rate is better expressed as 24 of 3707 (0.6%) birds, based on our total number of captures (including recaptured birds).

Predation events were not concentrated in any one of the three forests. The highest predation rate was on Mt Kenya, with 11 of 1315 (0.8%) captures predated. The rate for Kakamega [11 of 1869 (0.6%) captures] was lower, and that for Taita Hills [2 of 523 (0.4%) captures] was the lowest. However, the proportions of predation events per forest was not significantly different from those expected given the proportion of total captures per forest ($\chi^2 = 0.86$, 2 df, $P > 0.05$).

At the spatial scale of mist-netting sites and the temporal scale of days, predation was highly concentrated in space and time: a 'feeding-frenzy' effect. All predation events occurred in just 7 (23%) of our 31 mist-netting sites, significantly fewer than the 16 sites (mean of 5 simulations picking 24 captures randomly from the total of 3707 captures and assigning these to sites according to the number of captures per site) expected ($\chi^2 = 10.4$, 1 df, $P = 0.001$). Notably, no predation events occurred in the main Kakamega Forest, significantly fewer than the 4 expected based on the fact that 680 of our 3707 total captures were there ($\chi^2 = 4.8$, 1 df, $P = 0.03$). Furthermore, birds were killed on only 9 of 87 (10%) days in which mist-netting was carried out, making the predation rate on these days 24 of 698 captures, significantly more than the 5 of 698 predation events expected had predation been random across days ($\chi^2 = 91.2$, 1 df, $P < 0.001$). Multiple birds were found dead simultaneously in five cases, comprising 14 of 24 (58%) predation events, and in three of these cases, two birds were found simultaneously killed in the same net, comprising 6 of 24 (25%) predation events. Indistinct peaks in predation occurred in the late morning and mid afternoon, and most birds killed were trapped in the net's lower panels with none in the highest (fourth) panel.

There is no strong evidence that predators returned to the nets over multiple days (which would indicate "learning" the presence of the food source). The mean day of predation was day 2.6 out of 4 days netting in each site where predation occurred. Only two of the predation events could have involved predators returning the following day: an unidentified small mammal returning to our fourth net at Ikuywa, Kakamega, and a blue monkey returning to our second net-line at the same site.

Predators were probably attracted to nets by noise and activity of captured birds. While our overall capture rate was 0.64 birds per net-hour, the mean capture rate (# birds captured in net/time since previous net-round in hours) for nets from which birds were killed was more than three times greater at 2.11 birds per net-hour. This idea is supported by a strong bias in the prey taken towards Yellow-whiskered Greenbuls (*Andropadus latirostris*), which are noisy and relatively large (means of 24.6 ± 1.5 g in Kakamega and 25.1 ± 1.0 g on Mt Kenya). Of the victims with identifiable remains, 8 of 18 (44%) were Yellow-whiskered Greenbuls, significantly more than expected given the 854 (23%) individuals of the species amongst the 3703 total birds captured ($\chi^2 = 5.1$, 1 df, $P = 0.02$). Six victims were unidentified because there were only bloody holes left in the mist-nets, and/or we observed blue monkeys carrying off bird corpses.

The blue monkey was the most common predator, accounting for 17 of 24 (71%) predation events. It was also a common predator in Tanzania (Cordeiro 1994). The species occurs in the Taita Hills but did not take birds from our mist-nets there. We regularly mist-netted birds attendant on swarms of safari ants (tribe Dorylini), but lost only one bird to ants, a White-starred Forest-Robin (*Pogonocichla stellata*) in the Taita Hills. An unidentified small terrestrial mammal killed two birds in Kakamega. Two birds were killed by African Goshawks (*Accipiter tachiro*), both of which were captured alongside their victims. The goshawk at Chehe on Mt. Kenya was caught two other times at the site, and so it is possible that this same bird also killed the White-starred Forest-Robin predated at this site. The only predatory birds that we mist-netted without prey were a Red-chested Owlet (*Glaucidium tephronotum*), which is mainly an insectivore although it will take vertebrates (Zimmerman et al. 1996) in Kakamega; a Black Goshawk (*Accipiter melanoleucus*) which was observed to bounce out of a net in the Taita Hills; and another African Goshawk that was caught twice at a different Mt. Kenya site.

Occasional predation of birds caught in mist-nets is well known but it seems that the predation we observed was elevated in forest fragments. All of these predation events occurred in small forest fragments (Ikuywa 1450 ha, W. Malava 50 ha, Chawia 50 ha, Mbololo 200 ha, Chehe 240 ha, Ragati 30 ha, Muthira 35 ha) and not a single one in the main Kakamega Forest (10,000 ha). Elevated predation rates in forest fragments are usually explained by edge effects that allow generalist predators to access the forest (Murcia 1995), but in our case all of the predators were forest species. Alternative explanations could be that predators have been concentrated into the forest fragments by the deforestation of the surrounding areas or that predators in the fragments were more stressed or more habituated to human presence and thus more willing to feed opportunistically on birds in mist-nets. Whatever the reason, it is clearly important that ornithologists conducting mist-net surveys in tropical forest fragments pay particular attention to the danger of predation of birds caught in their mist-nets.

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Ornithological Literature

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THE BIRDS OF PARADISE PARADISAEIDAE. By Clifford B. Frith and Bruce M. Beehler, illus. by William T. Cooper. Oxford University Press, Oxford, U.K. 1998: 613 pp., 15 color plates, numerous ranges maps, sonagrams, tables, graphs, line-drawings, and black-and-white photographs. $80 (hardcover).—This sixth volume in Oxford University Press' "Bird Families of the World" monograph series maintains the level of excellence set by previous volumes. Written by two of the world's foremost Paradisaeidae research biologists, magnificently illustrated by one of the world's finest artists, and about a remarkable and fascinating family of birds, this book is truly extraordinary. A great deal of work went into the preparation of this volume. Frith and Beehler have spent years studying birds of paradise—they are senior authors of 85 of the references listed in the bibliography—and Frith made a five-month study-tour of the world's major institutional collections gathering information for the book. The result is a thorough compilation of what is known (and not known) about birds of paradise that will likely be the standard reference on the family for decades.

The book is divided into two parts. The first consists of 8 thematic chapters beginning with "The incredible birds of paradise—an introduction", followed by chapters that treat the history of discovery and study of the family, evolution and biogeography, ecology, reproductive behavior, nesting biology and parental care, the birds' place in human tradition and culture, and conservation. The Paradisaeidae is considered by the authors to include 42 species of 17 genera that live in New Guinea (38 species), Australia (2 endemic species), and the Moluccan Islands (2 endemic species). They reject recent attempts to reassess the family using the phylogenetic species concept that would increase the number of species to about 90. The authors' phylogenetic reconstruction was based on their cladistic analysis of 52 characters including anatomy, external morphology, plumage, behavior, and ecology. They divide the family into two subfamilies, the Cnemophilinae (the 3 wide-gaped species) and the Paradisaenae. They acknowledge the diversity of opinion concerning the systematics of the Paradisaeidae and review and discuss recent treatments. In the ecology chapter they discuss the families' dependence on tropical closed humid forests, habitat selection, the significance of rainfall to distribution, and a long section on diet and bird-plant interactions.

Birds of paradise have long been of interest to biologists because of their reproductive behavior. They figured prominently, for example, in Darwin's sexual selection theory. The family has both monogamous and polygynous species, the latter often exhibiting extreme plumage dimorphism and court or lek display mating systems. The role of birds of paradise in native human culture, the use of plumes in ceremony, ritual, trade, and finance, is fascinating reading, as are the rather bizarre stories of 16th century Europeans suggesting that birds of paradise are legless, never alight, but rather float about in the air, feed on dew, with females nesting on the backs of the males. The conservation chapter views problems at several temporal scales, and includes detailed suggestions for conservation strategies.

Part II of the book provides brief treatment of the family, subfamilies, and genera followed by species accounts and occupies most of the book (330 pp.). Species accounts include a listing of local native names for the species followed by a description of the adult male and female, subadult, immature, juvenile, and nestling plumages. Sections follow (in most accounts) on distribution, systematics, nomenclature, subspecies, weights and measurements, habitat and habits, diet and foraging, vocalization, mating system, courtship behavior, breeding, annual cycle, status and conservation, knowledge lacking and research priorities, and aviculture. Sonagrams and line drawings illustrating behaviors (usually display postures) sometimes are included, as well as an 'other' section. A range map depicts locations where birds have been observed or collected. Nine magnificent color plates depict all bird of paradise species and one plate depicts eggs of 20 species. Additional plates present color photographs of bird of paradise habitats and nidification and molt.

The book concludes with seven appendices, a glossary, a bibliography, and an index. The first appendix is really a 20 page chapter on hybrid birds of paradise. Apparently, birds of paradise have an unusual propensity for hybridization and hybrid specimens have frequently been described as new species, leading historically to some heated controversies. Two plates depict 15 presumed intergeneric and 7 intrageneric hybrid birds. The second appendix provides an annotated list and chronology of exploration and study of birds of paradise. The third appendix deals with molt in birds of paradise and is based on the examination of 4852 museum study skins. The fourth appendix summarizes the records of plant species eaten by birds of paradise and the fifth, published recordings of vocalizations. The sixth appendix provides a brief guide to where to see and study birds of paradise and the final appendix is a gazetteer.

In addition to being an exhaustive coverage of birds of paradise, the book is well organized and highly readable. Its greatest value may ultimately be heuristic—the opportunities for future research are clearly spelled out. I highly recommend this book; it is well written, informative, beautifully illustrated and concerns an extraordinarily interesting family of birds. I have been fortunate in seeing 27 species of birds of paradise in the wild, but this book makes me want to go back for more.—WILLIAM E. DAVIS, JR.

TROGONS, LAUGHING FALCONS, AND OTHER NEOTROPICAL BIRDS. By Alexander F. Skutch, illus. by Dana Gardner. Texas A & M University Press, College Station, Texas. 1999: 282 pp., 27 black-and-white text illustrations. $29.95 hardcover.—This latest collection of Skutch's life histories is even more heterogeneous than the title suggests, as it includes a chapter on "the birdlike monkeys" (marmosets and tamarins; Callitrichidae). Skutch admits that some of the material has appeared in his previous books, but is expanded here. The bibliography includes 16 Skutch titles from 1947 to 1985.The text begins with two pages of generalizations about the family Trogonidae. It then focuses on the species with which Skutch is most familiar: the Slaty-tailed Trogon (*Trogon massena*) and the Violaceous Trogon (*T. violaceus*) primarily based on his field observations. The former is noted for nesting in tunnels dug into arboreal termite nests, whereas the latter prefers large nests of paper wasps, probably feeding on wasp larvae and pupae. The next chapter deals with the wood-quails of the genus *Odontophorus*, the Black-breasted (*O. leucolaemus*), the Spotted (*O. guttatus*), and the Marbled (*O. gujanensis*), the only species of the genus that are found in Costa Rica. The third chapter is devoted to the Laughing Falcon (*Herpetotheres cachinnans*), which Skutch calls "guaco." He considers it a "friend" of small birds as the Laughing Falcon preys heavily on snakes but not on birds. Chapter four deals with the Rufous Piha (*Lipaugus unirufus*), an uncolorful member of the family Cotingadae.

Next comes a chapter on the Grayish Saltator (*Saltator coerulescens*), followed by an account of the White-eared Hummingbird (*Hylocharis leucotis*) based on observations in the Sierra de Tecpan, Guatemala, emphasizing its vocalizations (the chapter is entitled "The Tinkling Hummingbird"). Then comes a chapter on the Violet-headed Hummingbird (*Klais guimeti*). The hummingbirds continue with chapters on the Long-tailed Hermit (*Phaethornis superciliosus*) and the Long-billed Starthroat (*Heliomaster longirostris*). Next comes the Striped Cuckoo (*Tapera naevia*), a parasitic species. A list of known hosts of this cuckoo (pp. 100–101) contains the only scientific names of birds in the book although this information is sometimes given for plants and animals other than birds (reptiles, p. 197).

Skutch's prose is quite informal and readable, and he seldom descends to anthropomorphism. An exception occurs in his discussion of the voice of the Piratic Flycatcher (*Legatus leucophaius*): "These notes seems to be the self-revealing expression of a character lighthearted and shallow, bound by no ties."

The penultimate chapter is entitled "The Strenuous Lives of Migratory Birds." It contrasts various aspects of the life histories of migrant and resident species and includes several generalizations, to which exceptions can be readily found. For example (p. 197), "The newly arrived female [of a migratory species] builds a simple cup-shaped nest; time does not suffice of construction of the more elaborate nests that permanently resident birds take weeks to finish." An immediately obvious exception to the "simple cup-shaped nest" generalization is the migrant Baltimore Oriole (*Icterus galbula*).

Anyone familiar with Skutch's writings will know that his informal prose is deceptive in that there is more original information on bird behavior than in many more "scientific" sources.

The book ends with an epilogue: "The birds I love." As is doubtless true of all ornithologists Skutch is plagued by visitors asking which is his favorite bird. If he bothers to specify, he says "tanagers and woodpeckers" but he usually says, "I have many favorite birds, but I do not love all birds equally." The factor that most strongly influences his attraction to birds is not beauty but behavior.

The text illustrations by Dana Gardner are called "intricate line drawings" on the dust jacket flap, but they are rather clearly scratchboard, possibly supplemented with line drawing (see particularly the Rufous Piha, on p. 35). Most of the figures are relatively static profiles; a few of the birds are portrayed in flight. The most lively is that of the Great Kiskadee (*Pitangus sulphuratus*), flying just over a large snake. The Gray-headed Chachalaca (*Ortalis cinereiceps*) is perched on a windowsill, doubtless one of Skutch's captive birds. Skutch tells us that two chachalacas are the only birds that he has ever hand-raised.—KENNETH C. PARKES.

THE OYSTERCATCHER—FROM INDIVIDUALS TO POPULATIONS. Edited by John D. Goss-Custard. Oxford University Press, New York. 1996: 442 pp., 155 numbered figures, 23 tables. $115 (cloth).—How does loss of habitat affect bird populations? Can population impacts of habitat loss be scientifically predicted? This compendium of Oystercatcher (*Haematopus ostralegus*) studies (some spanning decades) by 25 accomplished contributors helps probe these profoundly important questions. Taken together, the works examine relationships between habitat loss and socio-biological, predation, and reproductive factors that affect Oystercatcher survival and reproduction in North Sea regions of Europe. The book is organized in two sections, the first (chapters 1–10) focusing mostly on adaptations for survival and reproduction at the individual level, and the second (chapters 11–13) aiming to build on information from Part I to model how habitat loss may affect populations.

Part I clearly shows that Oystercatchers have a complex sociobiology and ecology, including deferred maturity with gradually developing social skills (for example territorial dominance), long investments to develop skillful foraging, a large range of habitats (some of poor quality, some inland and some marine), food intake rates that vary with birds' experience, weather, prey behavior, habitat quality, presence or absence of other Oystercatchers, and so forth. Now mix these factors, all of which can affect individual survivorship differentially under differing conditions, with an array of complex parental and territorial behaviors, and try to understand what consequence habitat loss may have to populations.

The combined number of years the contributors to this book have invested in these studies—certainly measured in centuries—are testimony to the complexity of the task at hand, and even with this, it is clear that no definitive answers are forthcoming. But this book, a pioneering effort, is an awesome start.

Oystercatcher population size is presumably determined through a balance of density-dependent factors operating at the level of individuals (e.g., breeding production, survivorship) and environmental factors. Some of these factors are assessed in chapters of this book and to a certain extent can be numerically described in a model. Among many examples are relationships between breeding densities and ages of first breeding or of habitat selection and hatching success. But for overall goals of the model, far more detail needs to be learned.

Many readers may ask what is the relevance of this study of a European shorebird to their own ornithological work. The title says a lot, but I believe there is more. A quarter of a century ago I was awestruck and perplexed by some amazing similarities between 'social order' of the tropical oceanic terns I was studying, that of Antarctic penguins whose colonial biology I had just read about in a thesis by David Ainley, and the biology of a jay being studied by my mentor, Glen Woolfenden. And now with this book about Oystercatchers (of all things!) come inklings of growing order and comprehension. Read this book whether you study penguins, terns, or jays, and you will not regret it. But at its price, however, you may regret a decision to purchase it! Try your library.—BRIAN A. HARRINGTON.

RESEARCH AND MANAGEMENT OF THE BROWN-HEADED COWBIRD IN WESTERN LANDSCAPES. Edited by Michael L. Morrison, Linnea S. Hall, Scott K. Robinson, Stephen I. Rothstein, D. Caldwell Hahn, and Terrell D. Rich. Studies in Avian Biology No. 18. 1999. $18.00 (postpaid). ISBN 1-891276-06-9 (paper).—Total numbers of Brown-headed Cowbirds (*Molothrus ater*), North America's common brood parasite, have been about 40,000,000 individuals (high estimate) and Breeding Bird Survey data indicate their total numbers to be declining slightly. Since the beginning of the BBS, *Homo sapiens* in the U.S. has steadily increased from 194,302,963 in 1965 to 270,298,524 in 1998. Interest in brood parasitism has increased seemingly at the same rate and with it concern about effects of brood parasitism on stability of host populations. This volume on cowbird biology and management presents 33 papers from the proceedings of a symposium held 23–25 October 1997 in Sacramento, California. As promised by the title, all papers are about the biology or host interactions of Brown-headed Cowbirds (one also including Bronzed Cowbird, *M. aeneus*); most papers have western U.S. origins and all have at least a minor management slant in their presentations.

The volume is organized into three sections. Scott K. Robinson introduces the 13 papers of the section titled "Cowbird ecology: factors affecting the abundance and distribution of cowbirds." Papers in this section discuss cowbird-habitat associations as measured by censuses, habitat measurements, GIS predictions, and livestock and bison. James N. M. Smith provides introduction to the 15 papers in the section "The basis for cowbird management: host selection, impacts on hosts, and criteria for taking management action" with development of a rule of thumb to help decide when cowbird management programs should begin. Papers in this second section involve cowbird-host studies to measure impact of brood parasitism on host species' demographies. L. S. Hall and Steven I. Rothstein introduce the 5 papers of the last section, "Cowbird control: the efficacy of long-term control and proposed alternatives to standard control practices," and give appropriate caution to a seemingly obvious and simple solution to low host numbers.

With no intention to slight others, I mention two papers worthy of attention. The first paper reports on a 10 year study of Willow Flycatchers (*Empidonax trailii*) in Oregon ("Costs of Brown-headed Cowbird parasitism to Willow Flycatchers" by J. A. Sedgwick and W. M. Iko). The authors show great variation in parasitism rates through time and space and give measures of lifetime reproductive success of parasitized and non-parasitized flycatchers. The second paper reports the efforts to understand cowbird mating system, host selection, and cowbird fecundity and nesting success by integrating results of radio-tracking adult cowbirds and genetic analysis of their young ("A spatial and genetic analysis of cowbird host selection" by D. C. Hahn, J. A. Sedgwick, I. S. Painter, and N. J. Casna). The paper by Hahn and coworkers comes close to answering one basic question of cowbird biology still not understood: by what criteria are host nests sought and selected?

The volume is current and was prompt in its appearance. Brood parasitism is very difficult to study, especially for cowbirds that are not specialized in their host selection. Editorial commentary and most papers pose challenging questions for future work on the biology of cowbirds, host species, and their interactions. There is still much to learn. These proceedings provide a resource of recent data and direction for the future.—PETER E. LOWTHER.

ANIMAL VOCAL COMMUNICATION: A NEW APPROACH. By Donald H. Owings and Eugene S. Morton. Cambridge University

Press, Cambridge, U.K. 1998: 296 pages, 50 line diagrams, 4 half-tones, 5 tables. $54.95 (hardback).—Humans communicate using sound and we feel a special empathy for organisms that do the same: witness the multitude of "nature sound" and bird song CDs on the market these days. (How many "Field Guide to the Smells of North American Mammals" are available?) This might explain why so much research has been devoted to the study of vocal communication. Owings and Morton have produced an excellent review of previous work in this area and have introduced a new framework for studying vocal communication. They use the terms "managers" to describe the producers of signals and "assessors" to describe the animals that receive these signals. They use this terminology to underscore the role of assessment, which, they believe, has been underplayed in the study of vocal communication. The emphasis on assessment leads to some interesting insights. Signals are redefined as "acts deployed to capitalize on assessment systems" and the authors use many examples to make a strong case that the study of assessment provides the key to understanding vocal communication systems.

The book also places a heavy emphasis on the integration of mechanistic and evolutionary approaches to the study of behavior. The authors are ideally suited to this task: Owings is a psychologist who has worked on mammalian vocal communication and Morton is an ornithologist with a strong background in the study of natural selection. This academic cross-fertilization is most successful when the authors discuss communication from the perspective of regulatory systems. Here they integrate physiology, psychology, natural selection, and evolutionary history to produce some thought-provoking insights into how and why animals vocalize.

I have two minor complaints about the book. First, the book is heavily biased towards studies of vertebrates and might be better titled "Vertebrate vocal communication". Second, some of the more speculative (and interesting) ideas in this book are presented as conclusions rather than hypotheses. For example, the claim that "Endothermy led to complex social behavior and parental care which, in turn, added kin selection and selection for 'Machiavellian' intelligence . . . [which then] . . . ratcheted up the number and variety of vocal signals favored by selection" is a testable hypothesis about the historical origins of complex behavior. Unfortunately, scant data are presented in support of this hypothesis and contrary data (extensive parental care, kin selection, and complex communication in some ectotherms) are not discussed.

In the preface, the authors express a desire to inject new blood into the study of animal communication. This book meets this goal; it is full of stimulating, challenging, novel, eminently discussible ideas and I strongly recommend it to all those who study animal communication.—DAVID G. HASKELL.

WHERE TO WATCH BIRDS IN AUSTRALASIA AND OCEANIA. By Nigel Wheatley. Princeton University Press, Princeton, New Jersey. 1998: 448 pp., numerous maps and line drawings. $35 (hardcover).—Another in his series of "Where to watch birds" (previous volumes include South America, Africa, and Asia), this book is designed as a first point of reference for anyone planning a birding trip to Australasia or Oceania. In this it succeeds very well. The book is divided into sections that reflect political country boundaries (e.g., Irian Jaya and Papua New Guinea) or location (e.g., a number of islands and island chains have been grouped together under the headings "Micronesia" and "Polynesia"). The area encompassed is vast—from Australia and Irian Jaya in the west, the Mariana Islands, Hawaii and Midway Island to the north, Pitcairn Islands to the east, and Antarctica to the south. Further subdivision produced over 200 sites, sprinkled with more than 100 maps, and line-drawings of the more spectacular birds highlighted in the text. The introductory material, which tells you how to use the book, includes a list of the 100 bird families that occur in the region, with endemic families highlighted in bold-face type. A brief section deals with habitat diversity, another with country species lists that includes comparisons with other areas of the world, and several sections deal with endemic species and families. A brief chapter explores the enormity of the conservation problems that plague the area, particularly those resulting from human overpopulation and the introduction of non-native mammalian predators and herbivores.

Each country (or cluster of islands) is introduced with a summary of the interesting birds present, modes of transportation, accommodation and food, health and safety concerns, climatic conditions, and best time-of-year for visits, followed by brief discussions of the species, families, and endemics that the country offers. A brief "Expectations" section give the reader some general idea of what they might expect to see on, for example, a 25-day trip. The site descriptions that follow include "localized" and "other" endemics (endemic to the country, not the site), non-endemic specialties, and information of special interest (e.g., addresses or telephone numbers for information about pelagic trips). The chapters end with a list of pertinent addresses, books and papers and present an annotated list, grouped by region, of all the endemic species, and a list of "near-endemics."

Australia is the first country covered, with sites grouped by state, and occupies about a third of the book. Then follow chapters on Fiji, Samoa, Tonga, Hawaii, Irian Jaya, Micronesia, New Caledonia, New Zealand, Papua New Guinea, Polynesia, Solomon Islands, Vanuatu, and Antarctica.

Considering the vast scope of this book, I found the site guides generally well-done. They were largely up to date for the sites I have most recently visited in Australia and New Zealand. I compared the site descriptions for Two People's Bay and Broome, Western Australia; for Bruny and Maria Islands in Tasmania; Deniliquin, New South Wales, and Tiritiri Matangi Island in New Zealand to accounts in other birding guides I have used in the past (e.g., *The Complete Guide to Finding the Birds of Australia,* by Richard and Sarah Thomas, *Where to Find Birds in Australia* by John Bransbury, *Birds of New Zealand, Locality Guide* by Stuart Chambers) and found that Wheatley's descriptions compared favorably. Wheatley correctly states that Philip Maher in Deniliqun is the person to contact if you want to see a Plains-wanderer (*Pedionomus torquatus*) and provides a contact address and phone/fax number. Wheatley also provides a contact number for Philip Smith of Bravo Adventure Cruises, the man to contact if you want to see a Brown Kiwi (*Apteryx australis*) on Steward Island. Wheatley's advice on going to Tiritiri Matangi Island to look for Little Spotted Kiwi (*A. oweni*), Takahe (*Notornis mantelli*), and four other nearly extinct New Zealand birds is correct, and provides contact numbers for securing accommodations and a boat ride to the island. In Tasmania, Wheatley's site descriptions of Mt. Wellington, Bruny, and Maria islands should allow a visitor to see most or all of the endemics. I didn't find the Broome account as inspiring, but the all-important address and phone number for the Broome Bird Observatory is given.

Clearly, as the author emphasizes, this book, "is not meant to direct you to every site and bird in the minutest detail." It is, however, an indispensable book if you are planning a bird trip to this part of the world. It can be used to supplement other guides, some of which will have more detailed local site descriptions or more thorough coverage of specific areas. It isn't perfect and as the author points out, sites change with time—sometimes drastically. Don't expect too much from a book that treats such a vast area but certainly you should take a copy along if you are heading to Australasia—it is a relatively small book and will fit into your luggage.—WILLIAM E. DAVIS, JR.

HANDBOOK OF WESTERN AUSTRALIAN BIRDS. VOLUME I. NON-PASSERINES (EMU TO DOLLARBIRD). By R. E. Johnstone and G. M. Storr. Western Australian Museum, Perth. Available from: Western Australian Museum Bookshop, W. A. Museum, Francis St., Perth, WA 6000, Australia; Tel: (08) 9427–2779. 1998: 436 pp., 45 plates (42 in color), 30 color egg plates, 28 color photos (mostly habitat), numerous maps and line drawings. A$120 (hardcover).—This large format (23 × 31 cm), lavishly illustrated handbook, summarizes the current biological knowledge of the 360 species and subspecies of non-passerine birds that are found in Western Australia (which comprises about a third of the Australian land mass) and its adjacent seas. The last such attempt was *Birds of Western Australia* by D. L. Serventy and H. M. Whittell, published in 1948. Because of its large size and latitudinal spread, Western Australia is comprised of radically different climatic zones and their resultant zoogeographic zones comprise: a northern tropical fauna adapted to monsoonal summer rains and dry winters, a southwestern temperate fauna adapted to winter rains and dry summers, and a central arid zone fauna adapted to highly variable rainfall. The book begins with a chapter on physical features, climate, and vegetation. The climatic zones include: northern sub-humid and semiarid; southern semi-arid, sub-humid, and humid; separated by vast arid and desert zones. The discussion includes a full-page color map of primary vegetation types. Western Australia is then divided into four geographic land divisions: Kimberly (north), Arid Zone (majority of the state), South-west, and the Islands to facilitate a detailed discussion of land-forms, vegetation, climate, drainage patterns, etc. This section of the book is highlighted by 25 habitat photographs in color. A brief chapter presents the latest thinking about the origins of the Western Australian avifauna, tracing some elements back to pre-Gondwana break-up, and others to more complicated Asian derivations. The recorded 518 species consists of 382 breeding species (14 endemics), 125 non-breeding "visitors", and 11 non-native species. A chapter on migration and movements considers the typically complicated and poorly known patterns of nomadism, irruptions, and partial migrations. Interestingly, migrants include a significant northern Palearctic shorebird element and penguins and procellariids from Antarctica.

The bulk of this handbook (>300 pp.) is comprised of species accounts. These are based on the enormous database of over 1 million records, compiled by Storr from 1965 to his death in 1990. Each account begins with a detailed description of plumage and softpart coloration, and sections follow (usually) on distribution, habitat, status, food (and feeding), breeding, voice, and measurements. Where appropriate, a section on 'remarks' is included, often describing behavior. Occasionally, there is a full section on behavior or a section on relationships (e.g., describes other members of a superspecies). The status section frequently provides historical explanatory material (effects of rabbit plagues or farmer persecution). Most species accounts are accompanied by distribution maps but distribution is presented as a single tone of gray. Consequently, it is often necessary to read the status section to determine whether the map depicts breeding, non-breeding, or nomadic distribution. The species accounts effectively summarize what is known about the natural history of each species, although in some species the behavior descriptions are a bit skimpy. The species accounts lack in-text citations (a sacrifice to readability I presume), and hence it is often difficult to extract from the bibliography of nearly 500 references those dealing with a particular species.

The plates that accompany the text are generally excellent—I particularly like the richly colored plates by Martin Thompson. The plates provide, where appropriate, adult male and female, immature, and breeding and nonbreeding plumages. For the raptors and shorebirds, groups of species are depicted perching in one plate and flying in another, which facilitates interspecies comparisons. The 30 egg plates are photographs of eggs of about 200 species that breed in Western Australia and are of outstanding quality. The book concludes with a glossary, gazetteer, extensive bibliography, and an index to the bird species.

This is a thoroughly researched, beautiful and informative book that should be part of all academic libraries and owned by anyone with interests in Australian birds. At the present exchange rates of about US$0.64 = A$1.00, this book is not over-priced.—WILLIAM E. DAVIS, JR.

BIRDS OF KENYA AND NORTHERN TANZANIA: FIELD GUIDE EDITION. By Dale A. Zimmerman, Donald A. Turner, and David J. Pearson, illus. by Dale A. Zimmerman, Ian Willis and H. Douglas Pratt. Princeton University Press, Princeton, New Jersey. 1999: 576 pp., 124 color plates, numerous line drawings, ca 800 range maps. $39.50 (Paper)—*Birds of Kenya and Northern Tanzania* first appeared in 1996, to general acclaim. In a region very thin on good field guides, the book combined brilliant plates with authoritative and highly detailed text. Unfortunately, that comprehensiveness came with a cost, not just in dollars but in bulk and weight: after once hauling the book around in the field, many birders felt inclined to leave it sitting on the library shelf thereafter. Others simply hacked out the plates to carry as a field reference. This new, slim-line version, say the authors, was produced in order to stem such deplorable acts of vandalism. To be a touch cynical, one suspects that this more compact book is what the publishers would greatly have preferred in the first place—there certainly is no indication that the larger version will be reprinted.

Not that this 'field edition' is so teensy. It still weighs in at a couple of pounds and your safari jacket will need pretty impressive pockets to accommodate it. Nevertheless, it is without doubt a great deal more portable than its predecessor. To achieve this compression, substantial chunks of the old book have been jettisoned including the gazetteer, the bibliography, the Appendices listing Tanzanian and Ugandan bird species, and big tracts of the Introduction and glossary. There is no change in basic format, with brief text opposite each plate and more detailed information in a separate section of species accounts, an unusual layout for a modern field guide. The plates are identical in content, but shrunk to fit. Range maps have also shrunk, and are no longer included for the more localized species. The main changes, though, are in the species accounts themselves, which have been boiled down to essentials and, overall, reduced by about half. There is inevitably less detail than before, especially in the descriptions of behavior and ranges and the treatment of sub-species. Still, these 'essentials' remain, by field guide standards, very generous (and fully justify keeping the species accounts separate from the plates). There is plenty of substance here.

The new edition brings gains as well as losses. Four new birds to start with: the Kenya list has now crept up to 1084 species. Blank spaces opposite the plates are now filled with line drawings by Dale Zimmerman, a few recycled from the last edition but many new. All are delightful to look at; some, like the back view of the Pearl-spotted Owlet (*Glaucidium perlatum*) opposite plate 56, are genuinely useful; others seems a little superfluous (for example, the Hoopoe, *Upupa epops africana,* that joins three others of the same race on plate 61). There is a small amount of updated information in the text. I was pleased to see a much improved description of the voice of Pale-breasted Illadopsis (*Illadopsis rufipennis*) and some minor taxonomic revisions; the hapless Eastern Nicator, *Nicator gularis,* continues to yo-yo between families, bouncing back into the Malaconotidae from the Pycnonotidae.

Generally, however, little is added to the species accounts, which rehash and reduce the material from the earlier edition. The authors have done an impressive job of rendering down the old accounts while retaining their essence and this is also a gain for the field birder. The new text is concise, punchy, and to the point; because there is less detail to wade through, it is substantially easier to extract what one needs.

Though much diminished in size, the plates are eminently usable too. The careful layout of Zimmerman's designs (79 of the 125 plates) remains a joy to behold and perhaps even emerges more clearly on this smaller scale. The 'big' edition was distinguished by the exceptional crispness and accuracy of its color printing. Unfortunately, standards have slipped a little here. The plates are still good, but contours are fuzzier and the colors not as natural. This is most noticeable in several plates of mainly yellow and brown birds—the subtle hues of the greenbuls and female weavers, for example, are consistently over-saturated with yellows excessively orange and olive colors too brown. This is a pity but I doubt that it will cause any major difficulties with field identification; indeed the differences will probably only be noticed by those who have the earlier book available as a bench-mark.

Those working seriously on East African birds will be pleased to have the 'big' edition available on their shelves, as it still provides an extra and important layer of detail. In terms of usability, though, the field edition seems a clear case of 'less is more'. Any birder visiting the region will want this book close to hand. For Kenya and northern Tanzania, there is simply no competition, it leaves the others standing in a flurry of feathers. Elsewhere in East Africa, it will be an essential supplement to either van Perlo's *Illustrated Checklist* (which has very limited text) or the field guide by Williams and Arlott (which is out of date, with dismal illustrations). This field edition, more affordable and more portable, should give a major boost to birding and ornithology in this region, which has such a remarkably rich and fascinating avifauna. Altogether, very warmly recommended.—LEON A. BENNUN.

MARK CATESBY'S *NATURAL HISTORY* OF AMERICA: THE WATERCOLORS FROM THE ROYAL LIBRARY WINDSOR CASTLE. By Henrietta McBurney, with an introductory essay by Amy R. W. Meyers. Merrell Holberton Publishers, London. 1997: 168 pp., 110 illus., 60 in color (52 large color plates), 9" X 12" format. $40.00 (cloth).—The Print Room of the Royal Library at Windsor Castle houses literally thousands of historic drawings and watercolors, which reflect the interests of its royal collectors over the centuries. Among the collections acquired by King George III (in 1768) are the Catesby watercolors, which were executed by the Colonial American naturalist Mark Catesby (1682–1749), following his expeditions to the New World in 1712 and 1726, for his book *The Natural History of Carolina, Florida and the Bahama Islands* (published from 1731–1747). These watercolors were originally bound in three volumes and housed at the King's library in Buckingham House (Buckingham Palace), but were subsequently moved to the Royal Library at Windsor Castle by King William IV in the early 1830s. Through the generosity of a Japanese benefactor, Mrs. Hiroko Usami, a conservation project began in 1994 enabled the restoration of the watercolors and their subsequent exhibition in the United States from May 1997 to January 1999. I had the pleasure of seeing this wonderful exhibit at the Telfair Museum of Art in Savannah, Georgia, in March 1998. The exhibit is a selection of the Catesby preparatory drawings, executed in watercolor and gouache and are still in remarkably good condition.

Mark Catesby's *Natural History* remained the most authoritative work on the natural history, and particularly ornithology, of the New World until the publication of Alexander Wilson's *American Ornithology* in 1808–1814, but the monumental work of John James Audubon, 1827–1838, was of such a great artistic and scientific magnitude that all who came before quickly fell into obscurity and it is just now that Catesby is receiving the credit that is so fitting for this brilliant naturalist, explorer, and artist. Having published *Catesby's Birds of Colonial America* in 1985 (Chapel Hill; University of North Carolina Press; paper edition, 1999), I have been delighted to see the resurrection of interest in Catesby over the past decade. This beautiful volume represents the culmination of the renewed interest in Mark Catesby and is a fitting testimony to his mighty contribution to the natural history of the New World.

The front material of the book includes a Sponsor's Statement, Preface, Director's Foreword, Acknowledgments, an introduction, "The Perfecting of Natural History" by Amy Meyers, a section of the Windsor Volumes by Henrieta McBurney, and Note on the Natural History Albums of Sir Hans Sloane and Catalogue, both by McBurney. The main body of the volume consists of sections on birds (plates 1–17), fishes (18–23), crabs, turtles and corals (24–26), snakes, lizards and frogs (27–35), mammals (36–38), insects (39–40), and plants (41–52). Opposite each plate are annotations relating to the plate and comments on the animals and plants. The high quality paper and excellent color reproduction enhance the value of this important volume. The selections of plates is quite good and one is struck by the fidelity of the color of the first edition plates to the watercolors. Following Catesby's death, George Edwards (1693–1773) took over the *Natural History* and published a revised edition in 1754, which featured bright and unnatural colors. Thus, the first edition plates are easily distinguished from those of the second edition.

Mark Catesby was emphatically not the "Colonial Audubon" as he is often depicted; he was not at that level of artistic genius—nor was anyone else! Yet, Catesby was the father of New World natural history and he is certainly the father of American ornithology. This beautiful volume serves as a fitting tribute to that once forgotten great naturalist of the Colonial Period in North America, and I highly recommend it to anyone interested in the history of ornithology (or natural history) in the New World. Certainly, most academic libraries should have a copy.—ALAN FEDUCCIA.

THE BIRDER'S BUG BOOK. By Gilbert Waldbauer. Harvard University Press, Cambridge, Massachusetts. 1998: xi + 290 pp., 16 color plates, 62 line drawings, bibliography, index. ISBN 0-674-07461-0. $25.00 (cloth).—This well-researched, very attractive, and innovative volume fills the niche long left empty of placing birds and insects side-by-side in their ecological context. Waldbauer, professor emeritus of entomology at the University of Illinois at Urbana-Champaign, has aimed this book at birders and amateur naturalists and intentionally avoids professional jargon, making this an accessible book that deepens the birder's understanding of birds and the diversity of life.

The first 2 of the 10 chapters (each provided with bibliographical references) orient the reader to the evolutionary history of birds and insects and introduce insect anatomy and physiology (highlighted by detailed sketches). The following six chapters are playfully organized as an interplay between birds and insects and humans and insects, as each battles to consume and/or defend themselves from the other. First avian prey-seeking behaviors are explained ("avian eating habits" and "feeding guilds") and how birds exploit the ecological niches that insects occupy. Insects are then shown to counter birds' attacks with defenses favored by evolution such as camouflage, noxious chemicals, warning displays, and mimicry. The chapter describing how parasitic insects plague birds is followed by another that details birds' defenses against insects (anting, grooming behaviors, birds protected by insects, and adding green vegetation to nests). The pace of the book seems to pick up after the first four chapters, especially when the subject focuses on describing the ways that insects plague and parasitize people. Waldbauer succeeds in deepening our understanding of such a common, and unfortunately, intimate subject as our relationships with mosquitos, ticks, horseflies, chiggers, ants, and other biting and stinging insects. A brief history of our attempts to live with and control insects follows, noting the ecological consequences of past human errors in overusing insecticides and documenting wiser mosquito control based on knowledge of mosquito habits and the ecology of salt marshes.

"A Brief Guide to the Insects" is a systematic orientation to insects, describing each order's basic physiology and how they live, accompanied by illuminating line drawings by Jim Nardi. Although not intended as a field guide, its simple, clear language and fine illustrations will certainly facilitate identifying insects when using a field guide (listed in the bibliography) and "enable you to identify to the level of order about 98 percent of the insects that you see."

The final chapter, "Disappearing Diversity", discusses the history of extinctions as caused by the actions of humans: over exploitation, environmental pollution, the introduction of exotic organisms, and the destruction or alteration of habitats. Documenting the effect of declining migratory songbird populations on the growth of insect populations and noting the ecological implications, the author concludes that "birds are indispensable members of terrestrial ecosystems."

The author's ecosystem approach is based on his belief that to best understand any organism, one needs to view it "in the light of its ecological context, the plants, insects, and other organisms with which it associates." By placing insects and birds together in their ecological context, this book goes beyond being simply a "birder's bug book", ultimately seeking to show that we too are a part of this web of life; preserving biological diversity—including conservation of bird species—enriches our spirit and knowledge of ourselves. Waldbauer largely succeeds in this goal.

Birders will welcome this book and the opportunity to deepen their knowledge on the bird-insect relationship. It is clearly written, filled with beautiful drawings and instructive photos (readers will become endeared to the fledgling screech owl with moth in its beak) and based on a lifetime devoted to insect observation by an ornithologist at heart. An example of the attention to detail are the series of four different sketches located on the bottom right corner of each page showing a Pileated Woodpecker excavating a cavity in a tree. The four sketches are repeated throughout the entire book so that paging through the book sets the bird in motion. This book is a "must read" for birders and naturalists alike.—HOPE WOODWARD.

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THE WILSON BULLETIN

SUGGESTIONS TO AUTHORS

See Wilson Bulletin, 110:152–154, 1998 for more detailed "Instructions to Authors."

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THE WILSON ORNITHOLOGICAL SOCIETY

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A NEW SPECIES OF FLYCATCHER (TYRANNIDAE: *MYIOPAGIS*) FROM EASTERN ECUADOR AND EASTERN PERU

PAUL COOPMANS[1] AND NIELS KRABBE[2,3,4]

ABSTRACT.—A new species of New World flycatcher in the genus *Myiopagis* (Aves, Tyrannidae, Elaeniinae) is described from Andean submontane forest of eastern Ecuador and eastern Peru. It appears to be most closely related to *M. caniceps* of lower elevations and more distantly to *M. gaimardii,* with which it is syntopic. *Received 1 Dec. 1999, accepted 10 May 2000.*

The Tyrannidae, one of the World's largest avian families, harbors a vast array of confusingly similar species. Since the discovery that *Empidonax traillii* and *E. alnorum* are two partly sympatric sibling species with distinctive innate songs (Stein 1963, Traylor 1979, Kroodsma 1984), differences in suboscine vocalizations have increased in value as taxonomic characters (see Ridgely and Tudor 1994, Krabbe and Schulenberg 1997, Isler et al. 1998), inspiring field workers to learn to identify New World flycatchers by voice. We suspect that the growing knowledge of bird sounds in the Neotropics will shed further light on the taxonomy of the Tyrannidae, and as in this case, will lead to the discovery of additional species. Perhaps surprisingly, only seven New World flycatchers have been described from South America during the last two decades (Fitzpatrick and O'Neill 1979, Teixeira 1987, Graves 1988, Willis and Oniki 1992, Gonzaga and Pacheco 1995, Fitzpatrick and Stotz 1997, Schulenberg and Parker 1997).

In June 1992 P.C. tape-recorded and observed a flycatcher at an elevation of about 1000 m near Zamora in southeastern Ecuador (tape-recording archived at Library of Natural Sounds, Cornell Laboratory of Ornithology, LNS cat. no. 60232). He could not assign the vocalizations to any species he knew. By 1994 he had compared the vocalizations with all similar species and became convinced that the Zamora birds represented an unknown species. In October of that year we collected a pair near Zamora. N.K. later compared these specimens with all similar forms in the American Museum of Natural History (AMNH) and the Academy of Natural Sciences of Philadelphia (ANSP). In 1996 we collected two additional specimens, this time on the slopes of Volcán Sumaco, in northeastern Ecuador. All four Ecuadorian specimens are housed in Mu-

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[4] Corresponding author.

←

Frontispiece. Male and female *Myiopagis olallai.* Water color painting by M. Hoppe Wolf.

seo Ecuatoriano de Ciencias Naturales, Quito (MECN).

N.K. located an additional specimen in AMNH (cat. no. 819936) that had been collected in southern Peru and labeled as *M. gaimardii.* The five specimens clearly represent a distinct new taxon, which we name:

FOOTHILL ELAENIA

Myiopagis olallai, new species

Holotype.—MECN 6902, adult male collected by N. Krabbe and P. Coopmans on 23 October 1994 at Río Bombuscaro (04° 07′ S, 78° 58′ W) 5 km south-southeast of Zamora, Province of Zamora-Chinchipe, Ecuador, elevation 1000 m. Blood sample NK1–23.10.94, stored in Zoological Museum, University of Copenhagen.

Paratype.—MECN 6903, adult female collected together with the holotype. Blood sample NK2–23.10.94.

Diagnosis.—Sexes alike. Plumage similar to females of the sexually dimorphic *M. caniceps,* most closely resembling the Amazonian *M. c. cinerea,* but crown neutral gray instead of olive and coronal patch concealed and entirely pure white instead of semi-concealed and mostly yellow. Also like females of *M. caniceps absita* of Darién and *M. c. parambae* of western Ecuador and western Colombia, but differs by larger size; darker and faintly streaked instead of unstreaked breast; yellow instead of whitish lower throat; darker bill; darker back; and darker and pure gray crown, the latter being slightly tinged with olive in *M. c. absita* and *M. c. parambae,* especially on the nape. Differs from *Myiopagis gaimardii* by having a greener (dark olive green) back without any brownish wash; pure dark gray rather than gray-brown crown; shorter and broader crown feathers; pure white instead of yellowish white or pale yellow coronal patch; by having three well-defined instead of two ill-defined wingbars (*M. gaimardii* rarely shows faint traces of a third wingbar); by coronal patch being more concealed; and by having the white feathers of the coronal patch tipped with gray instead of blackish gray-brown.

Acrotarsal scutes less exaspidean (Ridgway 1901:328) than in *Elaenia* (Zimmer 1941a), reaching the posterior edge of the outer side of the tarsus only in its distal part and showing a broader plantar space between the acrotarsal edges on the inner side, slightly broader than in *Myiopagis caniceps* (Fig. 4). Plantar space smooth, lacking the small scutes on the inner side of the tarsal joint often indicated in *Elaenia* (Fig. 4) and well developed in *Pseudelaenia.* (Zimmer 1941b).

Description of the holotype.—Capitalized names and numbers of colors follow Smithe (1975). Male. Crown Dark Neutral Gray (83). Concealed crown patch white, all white feathers with gray tips. Back Olive Green (47). Wings Blackish Neutral Gray (82) washed with Olive Green (47) on the lesser coverts. Wing coverts with three well-defined bars that are slightly paler than Sulphur Yellow (57) and confined to the edges of tips of outer webs, on greater coverts 1 mm wide and tapering to points along outer edges 5 mm from tips, on median coverts 1.5 mm wide and tapering to points 3.5 mm from tips, on lesser coverts as diffuse spots, 1–1.5 mm wide, spots on inner lesser coverts washed with Olive Green (47). Tertials with well-defined, 1–2 mm wide, Sulphur Yellow (57) edges of outer webs. Secondaries narrowly edged Sulphur Yellow except for the basal 5 mm of their exposed parts. Primaries very narrowly edged Olive Green (47) except on the terminal 10 mm. A small, horny spur present at the edge of the wing near the tip of the alula. Tail slightly browner than wings and narrowly edged Olive Green (47). Lores, eye-ring, subocular region, and cheeks mottled gray and white. Throat whitish slightly mottled with gray. Rest of underparts, wing linings, and edges of inner webs of remiges, a little lighter and yellower than Sulphur Yellow (57), lower throat and especially breast clouded with Olive Green (46) producing a slightly streaked effect. Iris brown, bill and feet blackish, extreme base of underside of mandible brownish gray. Body mass 14.0 g. Light fat. Skull 10% ossified. No Bursa of Fabricius. Testes 2 × 4 mm. Stomach: 6 mm black beetle and 40 mm caterpillar. Wing, tail, and body molting (not affecting measurements). Wings 61 mm, tail 51 mm, tarsus 17.2 mm, bill from skull 12.3 mm, gonys 5.9 mm, bill height at fore edge of nostrils 3.3 mm, bill width at fore edge of nostrils 3.7 mm.

Description of the paratype.—Female. Sim-

TABLE 1. Measurements of the five known specimens of *Myiopagis olallai.*

Catalog no.	Sex	Body mass g	Wing flat mm	Tail mm	Tarsus mm
AMNH 819936	M		60	50	17.9
MECN 6902	M	14.0	61	51	17.2
MECN 7141	M	11.1	60	53	16.0
MECN 6903	F	12.0	59	47	17.0
MECN 7142	F	11.3	56	48	15.9

ilar in structure and coloration to the holotype. Iris brown, bill and feet blackish, extreme base of underside of mandible gray-brown. Body mass 12.0 g. Light fat. Skull 50% ossified. No Bursa of Fabricius. Ovary 6 × 2.5 mm, inactive. Oviduct straight. Stomach: two caterpillars. Tail and body molting (not affecting measurements). Wings 59 mm, tail 47 mm, tarsus 17.0 mm, bill from skull 12.0 mm, gonys 5.9 mm, bill height at fore edge of nostrils 3.2 mm, bill width at fore edge of nostrils 3.5 mm.

Additional material examined and variation in the series.—An adult male (MECN 7141) and a female (MECN 7142), were collected together in northeastern Ecuador (Napo Province, 00° 43′ S, 77° 38′ W, 1000 m) on 17 December 1996. They are similar to the types in coloration but are slightly smaller (see *Measurements*). The female is not fully adult, showing some buffy brown feathers on the nape and a buffy brown wash to the tips of most rectrices and wing-coverts. An adult male (AMNH 819936), collected in Peru (depto. Ayacucho, 12° 39′ S, 73° 40′ W, 890 m) by John S. Weske on 13 July 1966, also clearly represents *M. olallai.* It is virtually identical to the type, differing only by being paler (less olive) on the breast, by having slightly paler wingbars and wing panel, and by having a slightly lighter gray crown.

Measurements.—*Myiopagis olallai, M. caniceps cinerea,* and *M. g. gaimardii* are similar in measurements of body mass and length of wings, tail, and tarsi (Table 2), as well as in bill dimensions.

Vocalizations.—The song of *M. olallai* consists of an about 2 s long harsh trill at a rate of approximately 14 notes per second at 4–6 kHz, distinctly rising in pitch, and preceded by introductory notes that vary in number, pace, and rhythm (Fig. 1A–B). Introductory notes are of two types, one falling from 6 to 3.5 kHz and the other from 5 to 3.5 kHz. Sometimes short series of calls are given alone (Fig. 2A), but usually a series terminates in song (Fig. 1A–B). Both calls are distinct from the often heard, rhythmic call of *M. caniceps cinerea* (Fig. 2B) and from the single calls given by *M. c. caniceps* (Fig. 2C) and *M. gaimardii* (Fig 2D). Song and calls are given from middle and upper levels of the forest while the birds follow mixed-species flocks, most frequently in the morning.

TABLE 2. Comparative measurements of *Myiopagis olallai, M. caniceps cinerea* and *M. g. gaimardii.*

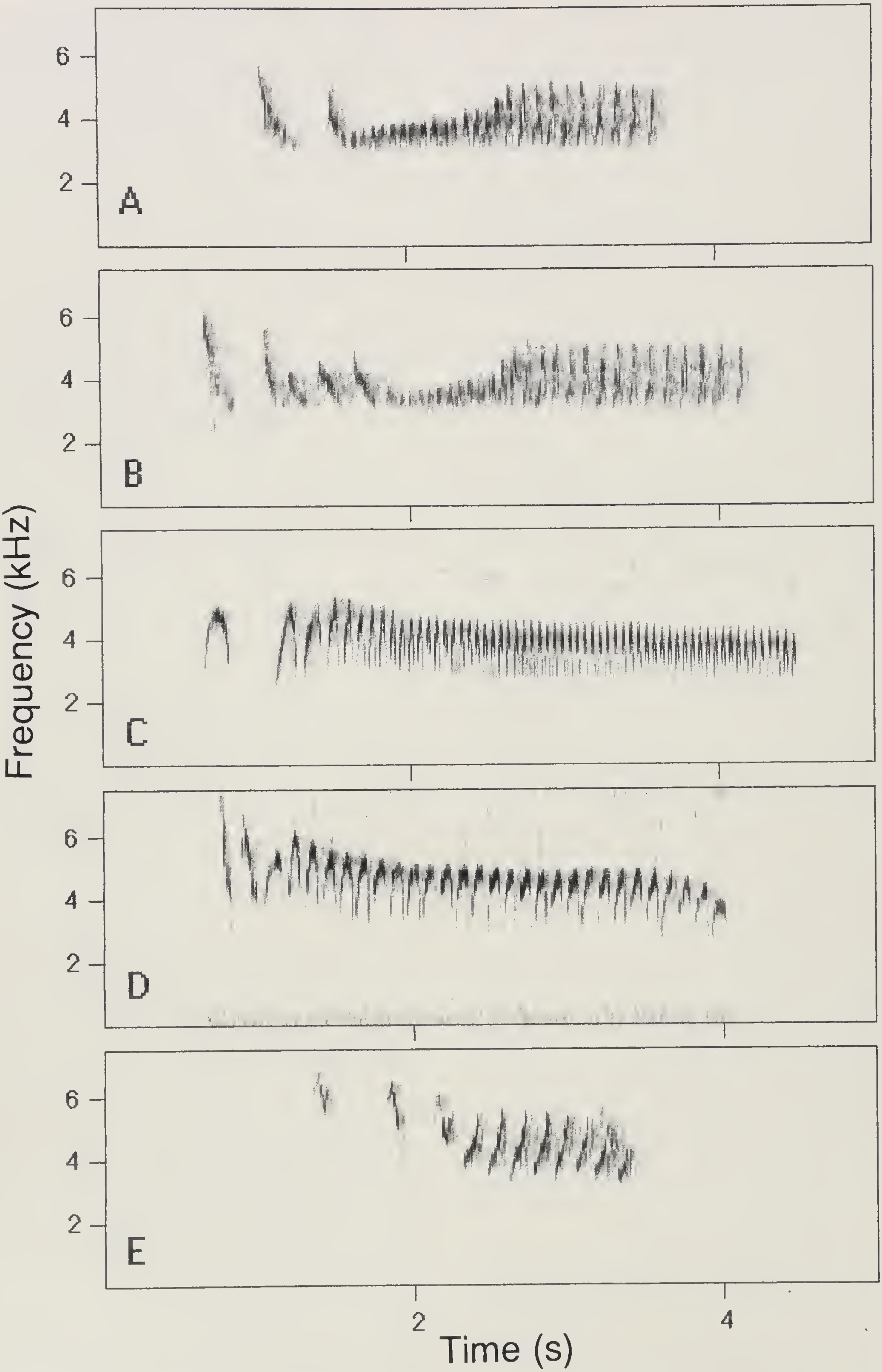
	M. olallai	*M. caniceps cinerea*	*M. gaimardii gaimardii*
Body mass			
males	12.6 ± 1.5[a] (11.1–14.0)[b] n = 2[c]	10.7 n = 1	12.5 ± 0.2 (12.3–12.7) n = 3
females	11.7 ± 0.4 (11.3–12.0) n = 2		12.0 n = 1
Wing flat			
males	60.3 ± 0.5 (60–61) n = 3	63.6 ± 2.4 (59–67) n = 9	62.3 ± 2.1 (58–66) n = 15
females	57.5 ± 1.5 (56–59) n = 2	58.0 ± 1.4 (56–59) n = 3	58.5 ± 1.7 (55–61) n = 13
Tail			
males	51.3 ± 1.3 (50–53) n = 3	52.8 ± 3.5 (48–59) n = 9	56.3 ± 3.5 (51–62) n = 15
females	47.5 ± 0.5 (47–48) n = 2	46.3 ± 1.2 (45–48) n = 3	51.1 ± 3.3 (45–56) n = 13
Tarsus			
males	17.0 ± 0.8 (16.0–17.9) n = 3	16.5 ± 0.7 (15.3–17.2) n = 8	17.7 ± 0.6 (16.7–18.6) n = 15
females	16.5 ± 0.6 (15.9–17.0) n = 2	15.8 ± 0.6 (15.0–16.4) n = 3	16.7 ± 0.5 (15.7–17.8) n = 13

[a] Mean ± Standard Deviation.

[b] Range

[c] Sample size.

The calls and songs of *M. subplacens, M. viridicata, M. flavivertex,* and *M. gaimardii* (Fig. 2D) differ strikingly from those of *M. olallai* in both quality and pattern (unpubl.


Frequency (kHz)
6
4
2
A
B
C
D
E
2
4
Time (s)

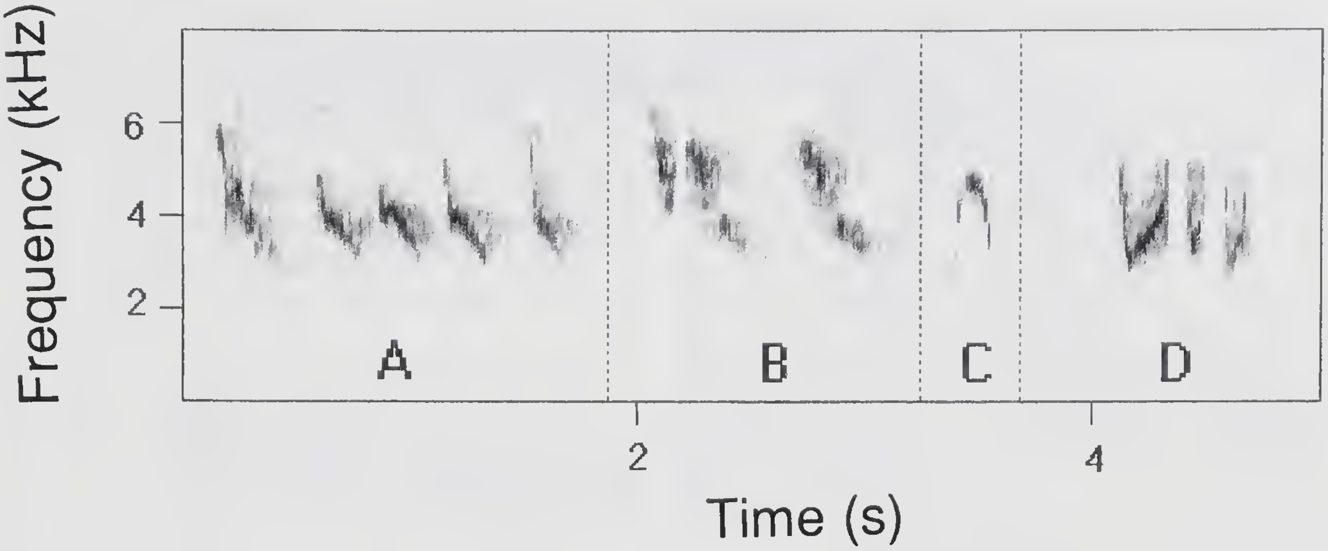


FIG. 2. Sonagrams of calls of *Myiopagis* New World flycatchers. A. *M. olallai* (type locality, P.C., June 1992); B. *M. caniceps cinerea* (Napo, eastern Ecuador, N.K., October 1994); C. *M. c. caniceps* (Río Grande do Sul, south-eastern Brazil, W. Belton, November 1975, LNS 19532); D. *M. g. gaimardii* (song?; usual call without last two short notes; Napo, eastern Ecuador, R. S. Ridgely, July 1994; Moore 1997).

data). Only *M. caniceps* has vocalizations that superficially resemble those of *M. olallai.* Both species have songs consisting of a long series of notes; the song of *M. olallai* is a harsh, ascending trill (Fig. 1A–B) and that of *M. caniceps* is a distinctly different gradually descending series of softer notes (Fig. 1C–E). The pace is about 14 notes per second in *M. olallai* (Fig. 1A–B), whereas for *M. caniceps* it varies from 6–8 notes in *M. c. parambae* (Fig. 1E) and 9–10 notes in *M. c. cinerea* (Fig. 1D) to 21 notes in *M. c. caniceps* (Fig. 1C).

Habitat.—In Ecuador *Myiopagis olallai* has been found only in and at the edge of very humid to wet primary submontane forest. *Myiopagis gaimardii* occurs in both humid and deciduous forests and forest edges (Ridgely and Tudor 1994), although in eastern Ecuador deciduous forest is not found.

Behavior.—Myiopagis olallai has been encountered on 25 occasions (pers. obs.; M. Lysinger, D. and M. Wolf, pers. comm.). All observations were of pairs accompanying mixed-species flocks of the canopy and midlevels. The birds frequently gave their distinctive song and calls (Fig. 1) and responded to playbacks of their song by immediately approaching and singing. The white crown patch was visible during a few sightings, but it usually remained concealed even when the bird was highly excited. While singing after playback of their song, they perched vertically, half way out to near the tips of horizontal twigs and 2–15 m above the ground. While foraging, they perched almost horizontally and usually cocked their tails slightly. They were generally very active and frequently made short outward or upward sallies, briefly hover-gleaning prey from the uppersides and undersides of foliage, moss, twigs, and branches.

Distribution.—Known from the foothills (890–1500 m) of the eastern slope of the Andes in Ecuador and Peru (Fig. 3). In Ecuador known from three sites on the south slope of Volcán Sumaco, Napo Province (00° 43′ S, 77° 33–38′ W, 1000–1500 m) and from near Zamora, Zamora-Chinchipe Province (1000 m; type locality). In Peru known from 6 km east of Luisiana, Río Apurímac, depto. Ayacucho (12° 39′ S, 73° 40′ W, 890 m).

Presumably also occurs in intervening are-

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FIG. 1. Sonagrams of songs of *Myiopagis olallai* and *Myiopagis caniceps*. A. *M. olallai* (type locality, P.C., June 1992); B. *M. olallai* (type locality, P.C., June 1992); C. *M. c. caniceps* (Río Grande do Sul, southeastern Brazil, W. Belton, November 1975, LNS 19532); D. *M. caniceps cinerea* (Napo, eastern Ecuador, N.K., October 1994); D. *M. caniceps parambae* (Pichincha, northwestern Ecuador, P.C., February 1995).

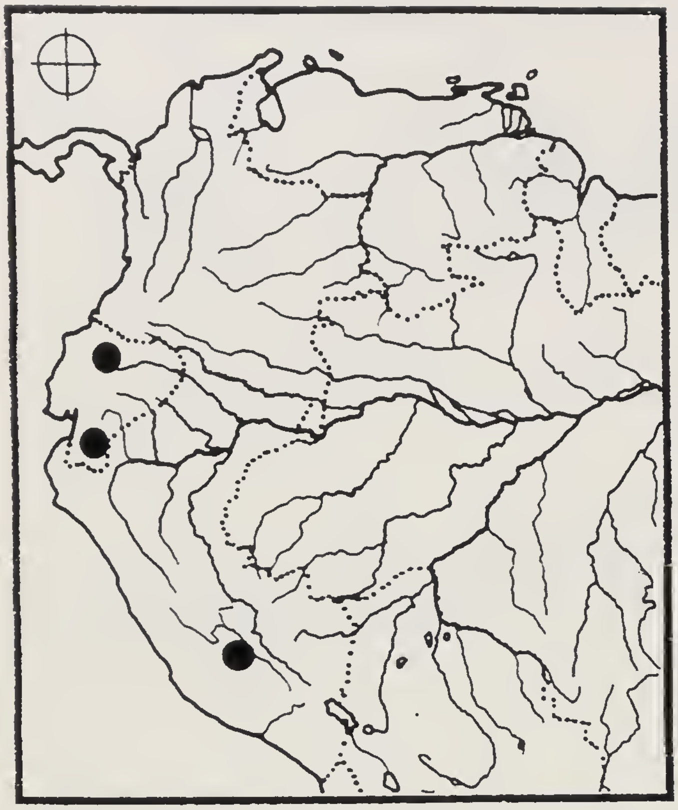

FIG. 3. Known localities of *Myiopagis olallai.* From north to south: Ecuador, Provincia de Napo, three sites in close proximity on the south slope of Volcán Sumaco (00° 43′ S, 77° 33–38′ W, 1000–1500 m); Ecuador, Provincia de Zamora-Chinchipe, 5 km south-southeast of Zamora, Río Bombuscaro (04° 07′ S, 78° 58′ W, 1000 m); Peru: Depto Ayacucho, Río Apurímac, 6 km east of Luisiana (12° 39′ S, 73° 40′ W, 890 m).

as, at least locally. More studies may reveal a wider elevational range, although the species appeared to be absent at Canelos, Pastaza Province, at 700 m elevation (pers. obs.). Like several other restricted range species, lower montane species of New World flycatchers (*Phylloscartes gualaquizae, Phylloscartes orbitalis, Zimmerius cinereicapillus, Hemitriccus rufigularis*), *Myiopagis olallai* is not known to range north of Volcán Sumaco in northern Ecuador, but few modern surveys have been undertaken in wet forests at similar elevations on the Amazonian slope in Colombia.

Myiopagis olallai is sympatric with *Myiopagis g. gaimardii,* which has been collected at Zamora, about 1000 m (3250 ft; AMNH 167583) and 6 km east of Luisiana, Río Apurímac, depto. Ayacucho (12° 39′ S, 73° 40′ W, 890 m elevation; AMNH 819932) and which was tape-recorded at 1100 m along the Narupa-Loreto road, just a few km from where *M. olallai* was collected. These are the highest records of *M. g. gaimardii* we found (AMNH, ANSP, unpubl. data). Further studies are needed to determine any ecological differences where the two species meet. Although preliminary observations indicate that in the zone of overlap, *M. g. gaimardii* may prefer more secondary habitats, more data are needed. Elsewhere in its range, *M. caniceps* has been recorded as high as 1200 m (Ridgely and Tudor 1994), but we can find no definite records of this species from higher than 500 m on the east slope of the Andes (LSUMZ, AMNH, ANSP, unpubl. data.).

Etymology.—Named in honor of the late Alfonso Manuel Olalla, in appreciation of his unparalleled contribution to Neotropical ornithology. Of the over 70,000 specimens (most are housed in American Museum of Natural History, New York and Swedish Museum of Natural History, Stockholm) he and members of his family collected, notably his father Carlos and brother Ramón, he collected the vast majority, in Venezuela, Colombia, Ecuador, Peru, Bolivia, and Brazil. These specimens form the main basis of our knowledge of the distribution and variation of birds in many of these areas, especially in Amazonia.

DISCUSSION

Taxonomy and speciation.—*Myiopagis olallai,* although well differentiated from congeners, is clearly a *Myiopagis,* exhibiting similar tarsal scutellation and possessing a small, horny spur at the edge of the wing near the tip of the alula, a character shared with only a few other tyrannid genera (*Zimmerius, Acrochordopus*; D. Agro, unpubl. data).

In external morphology *Myiopagis olallai* most closely resembles *M. caniceps* and *M. gaimardii.* It lacks the long, narrow shaggy crest feathers and ill-defined wingbars of *M. gaimardii.* The wing markings of *M. olallai* are strikingly similar to those of *M. caniceps,* and the quality of certain vocal notes also suggest that *M. caniceps* is the closest relative of *M. olallai* despite the lack of sexual dimorphism in the latter. We hope that future biochemical analysis will shed further light upon the taxonomic position of *M. olallai.*

Myiopagis caniceps itself consists of three song groups (Fig. 1C–E) that appear to coincide with the subspecies *M. c. cinerea* of

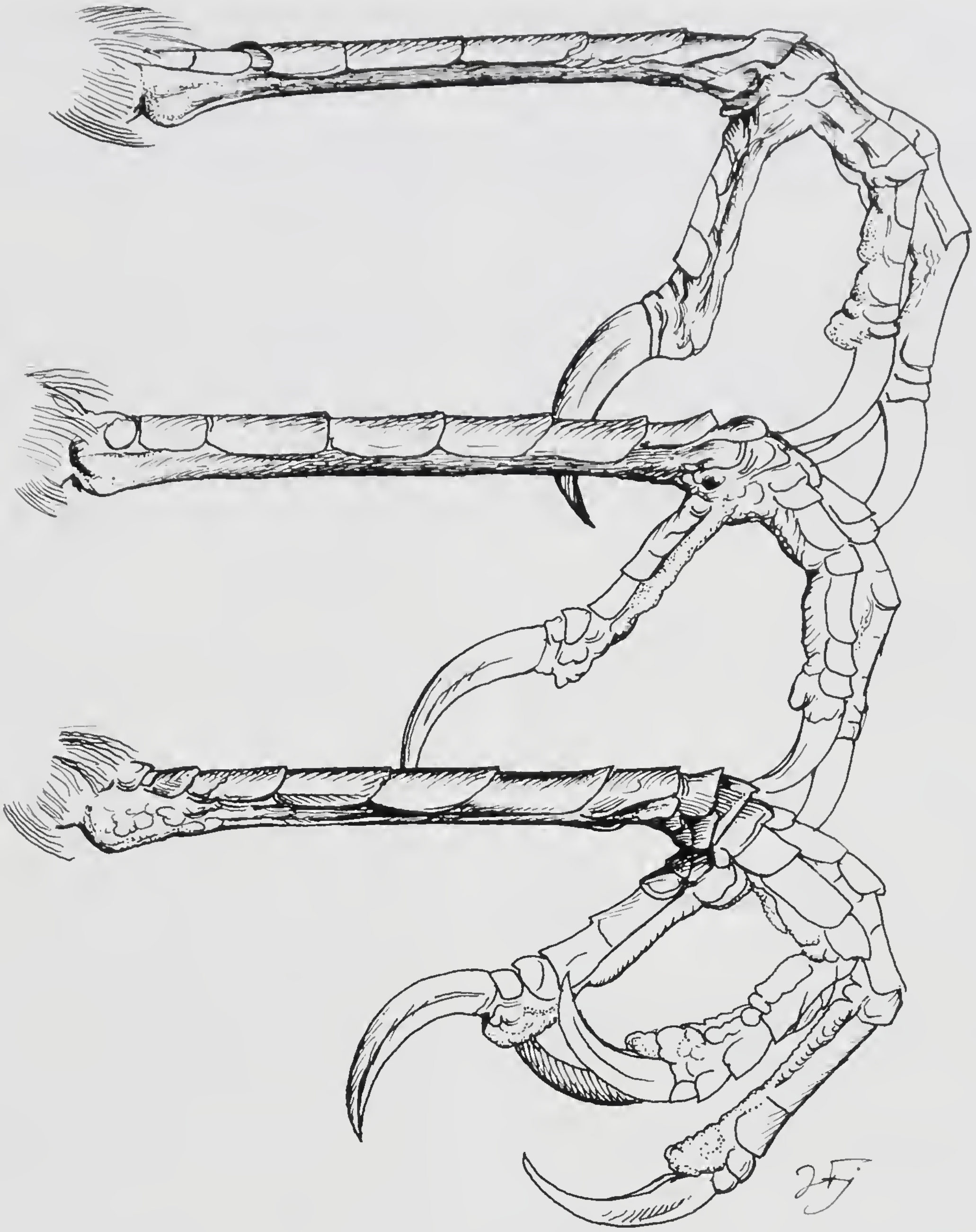

FIG. 4. Medial view of tarsus-metatarsus of *Myiopagis* and *Elaenia.* From top to bottom: *Myiopagis olallai, Myiopagis c. caniceps,* and *Elaenia albiceps griseigularis.* Drawing by J. Fjeldså.

Amazonia, *M. c. caniceps* from south-eastern Brazil and northern Argentina to Bolivia, and *M. c. parambae* of western Ecuador and Colombia (with *M. c. absita* of the Darién). They differ from each other to such an extent that species rank for each could be suggested following the guidelines of Isler and coworkers (1998). However, their pronounced sexual dimorphisms, unique in the genus, as well as qualitative similarities in their voice underline that they are more closely related to each other than to *M. olallai.* Because of our lack of sufficient data from elsewhere in South America, particularly in potential contact zones, we hesitate to change their traditional taxonomy.

Conservation.—Myiopagis olallai is known to occur in two national parks in Ecuador: Parque Nacional Sumaco-Galeras and Parque Nacional Podocarpus. Within these parks it only occurs at lower elevations, where the threat to the forest by invading settlers is most imminent. Forest at elevations occupied by *M. olallai* is disappearing at an alarming rate along the entire eastern slope of the Andes (see Robbins et al. 1992, Stotz 1999).

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NESTING RECORDS OF FIVE ANTBIRD SPECIES FROM THE COLOMBIAN AMAZON

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JUAN LUIS PARRA[1]

ABSTRACT.—Few nests of Amazonian antbirds (Thamnophilidae and Formicariidae) have been described. Here we present nesting records for five species of antbirds found in Tinigua National Park, Colombia. A pouch-shaped pensile nest of the Warbling Antbird (*Hypocnemis cantator*) in a treefall gap within seasonally flooded forest contained two eggs colored like those found in French Guiana but different from those in Amazonian Brazil and Peru. The Black-spotted Bare-eye (*Phlegopsis nigromaculata*) also nested in seasonally flooded forest; it constructed a cup-shaped nest inside a hollow rotten stump and laid two eggs. Two naked nestlings with bright yellow bills disappeared soon after hatching. Two cup-shaped nests of the Scale-backed Antbird (*Hylophylax poecilinota*) were in mature terra firme forest. Both contained two eggs similar in color to those of other subspecies; nestlings were naked and had conspicuous yellow bills. Those found in one nest disappeared 11 days after hatching. A nest of the Amazonian Streaked-Antwren (*Myrmotherula multostriata*) containing one egg was in seasonally flooded forest close to the river bank. This egg differed in coloration from others found in Brazil and from those of other members of the *M. surinamensis* complex, with which it was formerly considered conspecific. A Striated Antthrush (*Chamaeza nobilis*) nested in an unlined natural cavity some 3 m above the ground. The nestling closely resembled the adult but was smaller, had yellow bill commissures, and a shorter tail. *Received 29 Dec. 1999, accepted 8 May 2000.*

Little is known about the nests, eggs, and young of many of the antbirds (Thamnophilidae and Formicariidae) of lowland forests east of the Andes. Antbird species-level taxonomy is presently being reexamined using new techniques and analyses that include natural history information such as vocalizations (Isler et al. 1997, 1998, 1999). Data on reproductive biology of these species not only adds useful basic natural history knowledge, but could be important in studying systematics, phylogeny, and geographic variation of the group (see Zyskowski and Prum 1999).

Here we present nesting records for five antbird species that occur in a Colombian lowland rain forest in the upper Amazon basin. We describe the nests and eggs of the geographically variable Warbling Antbird (*Hypocnemis cantator*) and Scale-backed Antbird (*Hylophylax poecilinota*). We also describe the first nest and egg of the Amazonian Streaked-Antwren (*Myrmotherula multostriata*) found in Colombia, and offer the first complete descriptions of nest, eggs, and young of the Black-spotted Bare-eye (*Phlegopsis nigromaculata*) and the first nest and young of the Striated Antthrush (*Chamaeza nobilis*).

STUDY AREA

We made observations in a lowland tropical rain forest of northwestern Amazonia between the eastern Andes and the Sierra de la Macarena, on the eastern border of Tinigua National Park, Depto. del Meta, Colombia. Our study site, the Centro de Investigaciones Ecológicas Macarena (CIEM), is located on the western bank of Rio Duda (2° 40′ N, 74° 10′ W, 350–400 m elevation) and encompasses a variety of vegetation types (Stevenson et al. 1994, 1999). Low lying seasonally flooded forests are characterized by a discontinuous canopy dominated by *Guarea guidonia, Laetia corymbulosa, Ficus* spp., *Inga* spp., and *Cecropia* spp. with a dense understory primarily of *Heliconia* spp. Rolling hills dissected by streams support two types of terra firme forests; hill ridges are covered by mature forests with a continuous 20–25 m canopy with emergent trees to 30 m, while the lower eroded hill slopes, small valleys, and gulleys formed by creeks support open degraded forests with numerous vines, lianas, bamboo, and a dense understory. The temperature is relatively constant throughout the year (25° C), but precipitation (2600 mm annual mean) is strongly seasonal with a dry season from December through March and rainy season the rest of the year.

The CIEM supports a rich bird community with 441 species reported so far (Cadena et al. 2000). As with other Amazonian forest localities, a numerically important element of the study site's avifauna are the antbirds. To date, 51 species (47 Thamnophilidae and 4 Formicariidae) have been recorded.

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RESULTS AND DISCUSSION

Hypocnemis cantator flavescens or *saturata* (subspecies undetermined).—The Warbling Antbird is common in the thick undergrowth of seasonally flooded forests and less numerous in mature terra firme and open degraded forests at the CIEM. During routine bird censuses, we discovered an active nest of this species in seasonally flooded forest on the eastern bank of Rio Duda on 29 June 1997. The pouch-shaped pensile nest was located beside the trunk of a large recently fallen tree (Burseraceae) that had formed an extensive treefall gap in the forest. The nest was suspended about 1 m above the ground, attached in two points to a forked twig. A *Heliconia* leaf provided a roof over the nest and shielded it from view. The nest contained two pinkish eggs with purple streaks and spots, mostly on the large end. The eggs had not hatched by 6 July when we left the study site.

The *H. cantator* nest was similar in shape and placement to nests reported from other populations of this species, but there appeared to be variation in egg color. The eggs we found are similar to those of *H. c. notaea* of French Guiana (Tostain et al. 1992), but differ from those of *H. c. cantator* in Manaus, Brazil (white with brown spots, Oniki and Willis 1982) and of *H. c. collinsi* from the Rio Tambopata, Peru (white with brownish red specks and streaks, P. Marra, pers. comm.). Plumages of *H. cantator* also vary among populations, and species limits within *Hypocnemis* are being reconsidered (M. and P. Isler, pers. comm.). Further analyses using vocalizations, morphology, distribution, or molecular analyses may help to determine whether egg color variation is simply polymorphic variation or the result of some deeper evolutionary history.

Phlegopsis nigromaculata.—The Black-spotted Bare-eye, a "professional" ant-follower (Willis 1979), is a common attendant of ant swarms in open degraded and seasonally flooded forests at the CIEM, but is apparently absent from mature terra firme forests. On 30 June 1999 we observed two individuals carrying nest material in seasonally flooded forest and by 5 July the nest had been completed and contained two eggs. The nest was placed inside a 10 cm deep hollow rotten stump next to a small stream, 1 m above the ground (Fig. 1A). The cavity entrance was partially covered by leaves of an epiphytic aroid. The open cup nest was constructed of dry bamboo leaves and lined with small plant fibers. The eggs were vinaceous, heavily streaked, and spotted with purple (Fig. 1B); one measured 25.4 × 20.6 mm. Because the species is monomorphic, we were unable to determine if both sexes incubated but we observed at least two individuals near the nest during incubation. One egg hatched on 16 July, the other the next day. The chicks were completely naked and had yellow bill commissures (Fig. 1C). After heavy rains during the night of 17 July the stump broke apart and the nestlings disappeared. Subsequently, we collected the nest and deposited it in the ornithological collection of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN nest collection catalog #140).

Our observations on the microhabitat nest placement, nest architecture, and eggs of the Black-spotted Bare-eye are consistent with the scanty information from other parts of this species range. In southeast Peru, C. Munn [cited in Hilty and Brown (1986)] found two barely lined nests 0.3 and 0.5 m up in hollow tops of tree stumps.

Hylophylax poecilinota duidae or *lepidonota* (subspecies undetermined).—The Scale-backed Antbird is found regularly in mature terra firme forests, rarely in open degraded forests, and is absent from seasonally flooded forests at the CIEM. In recent years we found two nests of this species, both in mature terra firme forest. The first, found on 3 August 1996, was cup-shaped and located among the bases of the leaves of a live understory palm about 50 cm above the ground. It contained two pinkish white eggs with purple streaks and spots more concentrated on the large end. We observed both male and female incubating. The eggs had hatched by 5 August. The nestlings were completely naked and had yellow bills. We made no further observations on this nest.

We located a second nest on 20 April 1999 and observed it until 5 May. It was inconspicuously placed inside a 8.2 × 5.3 × 11.5 cm deep natural cavity in a live tree 22 cm above the ground (Fig. 1D). The cavity was wider inside than at the entrance and deeper than the base of the nest, but was full of de-

FIG 1. Antbird nests, eggs, and young found at the Centro de Investigaciones Ecológicas Macarena (all photographs by Gustavo A. Londoño). (A) Nest of the Black-spotted Bare-eye (*Phlegopsis nigromaculata*). (B) Eggs of the Black-spotted Bare-eye. (C) Black-spotted Bare-eye hatchlings. (D) Cavity containing a nest of the Scale-backed Antbird (*Hylophylax poecilinota*). (E) Eggs of the Scale-backed Antbird. (F) Scale-backed Antbird hatchlings. (G) Ten day old Scale-backed Antbird nestlings. (H) Nest of the Amazonian Streaked-Antwren (*Myrmotherula multostriata*). Photos are not to scale so size comparisons should not be made; see text for measurements. Color photographs in jpg format are available from the authors upon request via e-mail.

composing leaves. The entrance was partially covered by ferns and other understory plants. The 11.5 × 9.5 cm open cup-shaped nest was made of dry fibers and pieces of dry palm leaves. It contained two pinkish eggs heavily streaked and spotted with purple (Fig. 1E) that measured 19.1 × 15.2 mm and 19.0 × 14.7 mm. On the morning of 24 April, we found two hatchlings in the nest (Fig. 1F). The hatchlings' eyes were closed and their naked skin was grayish above and reddish below; the bill and soft palate were yellow. Three days after hatching, feather sheaths appeared on the wings and by days four and five on the head and back. By the tenth day, the chicks had their eyes completely open and were covered by gray down with two buffy wing bars (Fig. 1G). The nestlings were observed on the early morning of 5 May but by midday they were no longer in the nest. We could not determine if they fledged or if they were taken by a predator. Both male and female incubated the eggs and fed the chicks, but only the male was observed brooding them. We collected the nest after it was abandoned and deposited it in the ICN ornithological collection (catalog #139).

Nests have been reported from Pará, Brazil for *H. p. vidua* (Snethlage 1935, Pinto 1953) and French Guiana for *H. p. poecilinota* (Tostain et al. 1992). Plumages of *H. poecilinota,* especially those of the female, vary substantially among populations (Hellmayr 1929) yet the nests and eggs of the northwestern Amazonian form (*H. p. duidae* or *H. p. lepidonota*) appear to be similar to those from other populations.

Myrmotherula multostriata.—The Amazonian Streaked-Antwren was formerly considered a subspecies of *M. surinamensis,* but recent analyses of vocal characters, morphology, and distribution indicate that species status is merited (Isler et al. 1999). The English names proposed by Isler and coworkers (1999) were inadvertently reversed and *M. multostriata* should be the Amazonian Streaked-Antwren whereas *M. surinamensis* should be the Guianan Streaked-Antwren (M. and P. Isler, pers. comm.). At the CIEM *M. multostriata* is common in seasonally flooded forest, especially in the dense vegetation close to the bank of Rio Duda. On 4 July 1999 a male Amazonian Streaked-Antwren flushed by a Black Curassow (*Crax alector*) revealed the location of a nest about 40 m from the river bank. After being flushed, the bird sang its characteristic loudsong, confirming our initial species identification. The pouch-shaped pensile nest was firmly attached to two branches of a 40 cm tall seedling (Fig. 1H). Measurements of the nest were: external dimensions 80 × 65 mm, internal dimensions 52.5 × 38.6 mm, outside height 150 mm, depth 70 mm. The nest was composed of dry leaves (mostly *Heliconia* spp.), mosses, and thin plant fibers and contained one white egg spotted and streaked with purple. Five days later, the egg was gone, probably taken by a predator. We deposited the nest in the ICN ornithological collection (catalog #138).

Egg coloration in *M. multostriata* appears to be variable. The egg we found at the CIEM is similar to eggs of this species found in Pará, Brazil (white with brownish purple sprinkles and spots, Pinto 1953), but differs in coloration from other eggs from that same locality (white with black spots, Snethlage 1935). It is also different from the eggs of the Pacific Antwren (*M. pacifica,* formerly considered conspecific with *M. multostriata*), which are grayish white heavily speckled, mottled, and washed with shades of cinnamon-brown, with a heavier wreath around the large end in Panama (Stone 1918) or white with a faint tint of buff, spotted heavily on the larger end with dark brown in Antioquia, Colombia (Wetmore 1972).

Chamaeza nobilis.—The Striated Antthrush is rare at the CIEM, having been recorded only a few times during several years of field work. On 20 June 1997 we captured an adult Striated Antthrush in a mist net in mature terra firme forest. While taking the bird out of the net, another individual called constantly from inside a natural cavity in a tree next to the mist net. The following day, we inspected the cavity but the calling bird, a juvenile Striated Antthrush, was outside on the ground and continued to vocalize persistently. It resembled the adult but had yellow bill commissures and the rectrices were not yet fully grown. When we approached the bird, which was noticeably stressed by our presence, it did not attempt to fly but walked away, indicating that perhaps its wings were not yet suited for sustained flight. The nest cavity was 30 cm deep and located in a live tree approximately 3 m above the ground. Inside we found some feathers but no egg shells, plant fibers, leaves, or any other sign of a nest.

Relatively little is known about the nesting of species in the genus *Chamaeza.* As with the Striated Antthrush, the Rufous-tailed Antthrush (*C. ruficauda*; K. Zyskowski, pers. comm.) and Short-tailed Antthrush (*C. campanisona*; Bertoni 1901, Canevari et al. 1991) nest in natural tree cavities close to the ground. However, these species build a nest, typically a loose platform of dry leaves and fungal rhizomorphs.

Based on our observations and those of other researchers, geographic variation appears to be widespread in antbird egg coloration. It is important for studies of evolution and natural history that researchers determine the extent of this variation (see Sheldon and Winkler

1999) and continue to publish their observations and collect reference material.

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FEEDING BEHAVIOR AND FOOD HABITS OF WINTERING HARLEQUIN DUCKS AT SHEMYA ISLAND, ALASKA

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ABSTRACT.—The foraging ecology of wintering Harlequin Ducks (*Histrionicus histrionicus*) is poorly understood and information on basic food habits is lacking for this species in the Aleutian Islands of Alaska where the largest winter concentrations occur. We investigated feeding behavior and food habits of wintering Harlequin Ducks in the western Aleutian Islands of Alaska with respect to sex and temporal and environmental variables to document behavioral responses to winter conditions, resource use, and nutritional requirements. We found that on average, Harlequin Ducks spent most of the diurnal period feeding (70% males, 76% females). However, more time was spent feeding during evenings, midwinter, cold weather, and high tides. Gastropods, crustaceans, and diptera larvae made up 83% of the diet, but diet composition changed throughout winter. Despite change in food habits, diet energy density was stable throughout winter. *Received 29 Oct. 1999, accepted 5 March 2000.*

Wintering waterfowl have evolved a broad range of feeding adaptations (Korschgen et al. 1988), but temporal and environmental factors influence the way they meet energetic requirements most efficiently (Paulus 1988). To understand foraging patterns in winter, researchers have investigated the response of waterfowl feeding behavior to time of day (Campbell 1978, Bergan et al. 1989, Paulus 1984), season (Paulus 1984, Rave and Baldassarre 1989), temperature (Nilsson 1970, Sayler and Afton 1981), and tide (Nilsson 1972, Petersen 1981). Such relationships help explain how waterfowl adapt to their local conditions.

Basic information on foraging ecology and food habits of Harlequin Ducks (*Histrionicus histrionicus*) is lacking in the Aleutian Islands of Alaska where the largest wintering populations occur (Bellrose 1976). Although winter time budgets and food habits were measured for Harlequin Ducks in Newfoundland (Goudie and Ankney 1986), intraspecific differences in feeding among wintering waterfowl suggest that the effects of temporal and environmental variables cannot be generalized throughout a species' range (Paulus 1988).

Temperate waterfowl in high northerly latitudes may have little flexibility in their feeding schedules because of fluctuating winter conditions (Thompson and Baldassarre 1991). Therefore, information on the diurnal and seasonal foraging behavior of Harlequin Ducks may identify feeding periods crucial to the survival of this species in the Aleutian Islands. We investigated winter feeding behavior and food habits of Harlequin Ducks with respect to sex and temporal and environmental variables to document behavioral responses to winter conditions, resource use, and nutritional requirements.

METHODS

Study area.—Shemya Island is located in the western Aleutian Islands of Alaska, approximately 2575 km southwest of Anchorage (52° 43′ N, 174° 07′ E; Fig. 1). Bounded by 22 km of shallow, rocky coastline, Shemya Island provides winter feeding habitat for approximately 500 Harlequin Ducks. Temperatures on site are moderated by the maritime climate, but high winds, fog, and snow are typical in winter months. Shemya Island is part of the Alaska Maritime National Wildlife Refuge and is currently leased to the U.S. Air Force. A coastal access road affords clear visibility of nearly the entire coastline and facilitates observational studies.

Time budgets.—We used the focal flock scan sampling method (Goudie and Ankney 1986, Baldassarre et al. 1988) to estimate Harlequin Duck diurnal time budgets at 6 coastal sites from December 1995 to March 1996 and November 1996 to January 1997. We used a stratified random process to select the time and location of observation sessions; therefore, each site was visited during each of 3 equal diurnal periods (morning, afternoon, evening) once every 3 days. To sample behavior from 30 min before sunrise to 30 min after sunset, we adjusted the start and end times of diurnal periods biweekly to compensate for seasonal changes in day length. We divided observations into three winter stages for analysis: early winter (1 Nov–20 Dec), midwinter (21 Dec–9 Feb), and late winter (10 Feb–1 Apr).

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FIG. 1. Location of Shemya Island (52° 43′ N, 174° 07′ E) in the western Aleutian Islands of Alaska.

We recorded behaviors of males and females separately in randomly selected focal flocks (one or more birds within 10 m of one another) every min during 1093 30-min sessions. If the focal flock separated into 2 or more groups, we continued observations on one randomly selected group. We employed switch sampling (Losito et al. 1989) when focal flocks were obscured for 2 consecutive scans. We categorized behaviors as feeding, locomotion, resting, preening, and other (flight, agonistic, pair bonding; Paulus 1988). When individuals did not dive or head-dip for more than 2 min, we recorded their behavior as resting. The proportion of time engaged in a behavior was estimated by dividing the sum of birds in each behavior category per session by the sum of birds in all categories per session (Goudie and Ankney 1986). Diurnal percent time spent feeding (percent time feeding) was calculated as the sum of dive, head-dip, and pause proportions. We estimated total diurnal hrs feeding/day by multiplying the proportion of day spent feeding by hr of daylight. We also recorded temperature and tide height before each 30 min observation session.

Accurately estimating time spent feeding by large flocks of diving ducks is problematic because of the difficulty in tallying submerged birds (Baldassarre et al. 1988). Most Harlequin Duck flocks at Shemya, however, were comprised of 1 or 2 birds and rarely more than 6 (Byrd et al. 1992, Meehan 1997) so we had little difficulty determining the proportion of diving birds in a flock during a scan.

We analyzed diurnal time budgets with parametric statistics after subjecting nonnormal percentage data to arcsine transformation (Zar 1984). We used the Shapiro-Wilk *W* test to confirm that behavior variables (percent time feeding, resting, in locomotion, and preening) satisfied the assumption of normality following data transformation ($P > 0.05$). We used observation session as the sample unit to determine the relationship between dependent (behavior category) and independent (sex, diurnal time period, winter stage, temperature, tide, and day length) variables. We identified sex differences with independent *t*-tests and diurnal period and winter stage differences with ANOVA and Tukey's multiple comparison of means in a randomized block design (observation sites = blocks). We then used correlation analysis to identify significant correlations between behavior and environmental variables (tide, temperature, day length). To determine if regression slopes differed by sex, we included sex as an indicator variable and tested for interaction effects between sex and environmental variables in each behavior category (Kleinbaum et al. 1988). All statistical calculations were performed on an IBM compatible personal computer using Stata 5.0 for Windows (StataCorp. 1997). Results are presented as means ± SE.

Food habits.—To assess winter diet, we collected 43 actively feeding (observed >10 min before shooting) Harlequin Ducks (22 male, 21 female) from December 1995 to March 1996 and November 1996 to March 1997. Immediately following collection, we removed all contents of the upper digestive tract (esophagus and proventriculus) and stored them in 70% ethyl alcohol (Swanson and Bartonek 1970). We used standard taxonomic keys to identify prey items (Bulycheva 1957, Gurjanova 1962, Pavlovskii 1966, Barnard 1969, Schultz 1969, Abbott 1974, Tsvetkova 1975, Fauchauld 1977, Kozloff 1987) and estimated gross energy density (kJ g^{-1} dry weight) of esophageal and proventricular contents using published energy equivalents (Brawn et al. 1968, Cummins and Wuycheck 1971, Thayer et al. 1973, Reinecke and Owen 1980, Jorde and Owen 1988a). We limited our analysis to the upper digestive tract because differential digestion rates bias soft- and hard-bodied food items in the gizzard (Swanson and Bartonek 1970). We report aggregate percent dry mass (proportional mass of a given item in each bird averaged over all birds) and frequency of occurrence (birds with given food item/total birds; Bartonek and Hickey 1969, Swanson and Bartonek 1970, Swanson et al. 1974).

To analyze food habits we used the Wilcoxon rank-sum test and Kruskal-Wallis ANOVA to detect differences in each prey class by sex and winter period. We tested for differences in gross energy density of the diet by sex and seasonal period with parametric ANOVA.

RESULTS

Time budgets.—Feeding behavior of Harlequin Ducks varied by sex and by temporal and environmental variables. Although both sexes fed during most of the diurnal period (Table 1), females spent more time feeding than males ($t_{1091} = -5.46$, $P < 0.001$; Fig. 2). In contrast, males spent more time than females in locomotion, resting, and preening ($t_{1091} = 7.38$, $P < 0.001$; $t_{1091} = 4.00$, $P < 0.001$; $t_{1091} = 2.56$, $P = 0.011$; Table 1).

Changes in Harlequin Duck feeding behavior were apparent among temporal variables. Both sexes concentrated feeding bouts in the evenings (male: $F_{2,561} = 10.13$, $P < 0.001$;

TABLE 1. Diurnal time budget of Harlequin Ducks at Shemya Island, Alaska, during winters 1995–1996 and 1996–1997.

Sex	Winter stage[a]	Diurnal period[b]	n[c]	% of time[d,e] Feeding	Locomotion	Resting	Preening
Male	Early	Morning	64	63.7 (3.0)[f]	12.7 (1.5)	18.7 (2.2)	4.8 (1.0)
		Afternoon	61	70.6 (3.0)	7.2 (1.0)	17.9 (2.2)	4.0 (0.9)
		Evening	64	79.5 (3.1)	7.4 (1.4)	10.5 (2.1)	2.4 (0.6)
	Mid	Morning	63	76.4 (2.4)	8.7 (1.1)	11.7 (1.7)	2.7 (0.6)
		Afternoon	57	66.9 (3.7)	8.2 (1.1)	17.8 (2.6)	6.2 (1.6)
		Evening	53	79.5 (3.0)	6.1 (1.0)	11.7 (1.8)	2.6 (0.5)
	Late	Morning	70	60.2 (3.2)	12.9 (1.4)	20.9 (2.5)	5.0 (0.7)
		Afternoon	70	67.3 (2.9)	8.4 (0.9)	17.6 (2.0)	6.4 (1.2)
		Evening	69	69.5 (2.9)	8.3 (1.0)	16.7 (2.4)	5.2 (0.8)
Female	Early	Morning	57	77.4 (3.0)	6.2 (1.1)	12.3 (2.1)	3.8 (1.2)
		Afternoon	52	75.7 (3.8)	3.6 (0.8)	15.8 (2.7)	4.4 (1.5)
		Evening	55	79.9 (3.9)	5.1 (1.3)	9.8 (2.1)	4.8 (0.6)
	Mid	Morning	58	84.1 (2.6)	4.6 (0.7)	8.9 (2.0)	2.2 (0.6)
		Afternoon	50	74.1 (4.4)	5.0 (1.0)	15.5 (3.1)	5.2 (1.5)
		Evening	55	87.4 (2.2)	3.6 (0.6)	7.2 (1.7)	1.8 (0.5)
	Late	Morning	69	70.7 (3.2)	9.0 (1.2)	15.3 (2.6)	4.5 (0.9)
		Afternoon	64	75.5 (2.9)	4.8 (0.7)	15.4 (2.4)	3.9 (0.7)
		Evening	62	74.5 (3.3)	5.8 (0.9)	14.8 (2.6)	4.6 (1.0)

[a] Early winter (1 Nov–20 Dec), midwinter (21 Dec–9 Feb), late winter (10 Feb–1 Apr).

[b] Sampling occurred during three equal diurnal time periods from 30 min before sunrise to 30 min after sunset. The duration of these periods was adjusted biweekly to compensate for changes in day length.

[c] Sample unit was each 30-min observation session.

[d] Feeding, locomotion, resting, and preening accounted for >99% of diurnal activity.

[e] Activity budget is reported as percentage of diurnal period.

[f] SE in parentheses.

female: $F_{2,512} = 3.71$, $P = 0.025$; Table 1). As winter progressed percent time feeding increased and then decreased for both sexes (male: $F_{2,561} = 7.56$, $P < 0.001$; female: $F_{2,512} = 8.78$, $P < 0.001$; Fig. 2, Table 1). Despite a decrease in percent time feeding, total hrs feeding/day increased in late winter (male: $F_{2,561} = 24.35$, $P < 0.001$; female: $F_{2,512} = 32.33$, $P < 0.001$), probably the result of a 72% increase in day length (Fig. 2).

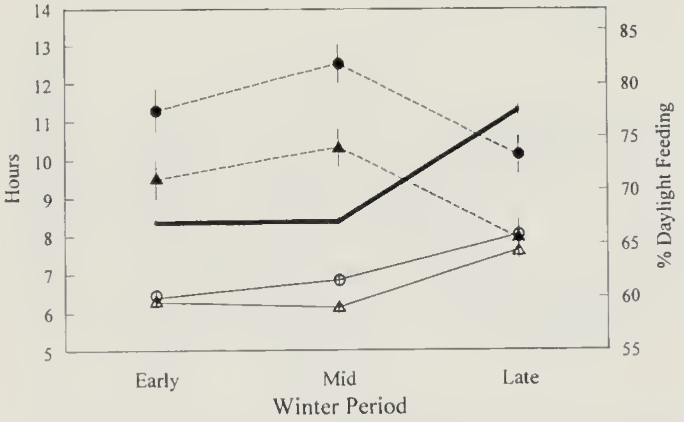

FIG. 2. Percentage of daylight time spent feeding (dashed lines) and total hr feeding (solid lines) relative to length of day (thick solid line) during three winter periods. Males and females are represented by triangles and circles, respectively. Error bars indicate ± standard error.

Tide, temperature, and day length also were correlated with Harlequin Duck behavior. Behavior was not affected by tide direction ($t_{1091} = 0.31$, $P > 0.05$), but tide height was positively correlated with percent time feeding ($F_{1,1091} = 18.77$, $P < 0.001$) between both sexes equally (no interaction with sex; $F_{1,1089} = 0.90$, $P > 0.05$). Conversely, temperature was negatively correlated with percent time feeding ($F_{1,1091} = 8.07$, $P = 0.005$) between both sexes (no interaction with sex, $F_{1,1089} = 2.68$, $P > 0.05$). Day length, too, was negatively correlated with percent time feeding ($F_{1,1087} = 60.69$, $P < 0.001$) between both sexes (no interaction with sex, $F_{1,1085} = 0.25$, $P > 0.05$).

Food habits.—The winter diet of Harlequin Ducks consisted of 49 prey taxa from 10 classes (Table 2). Principal diet classes included gastropods (primarily *Littorina sitkana*), crustaceans (predominately gammerid amphi-

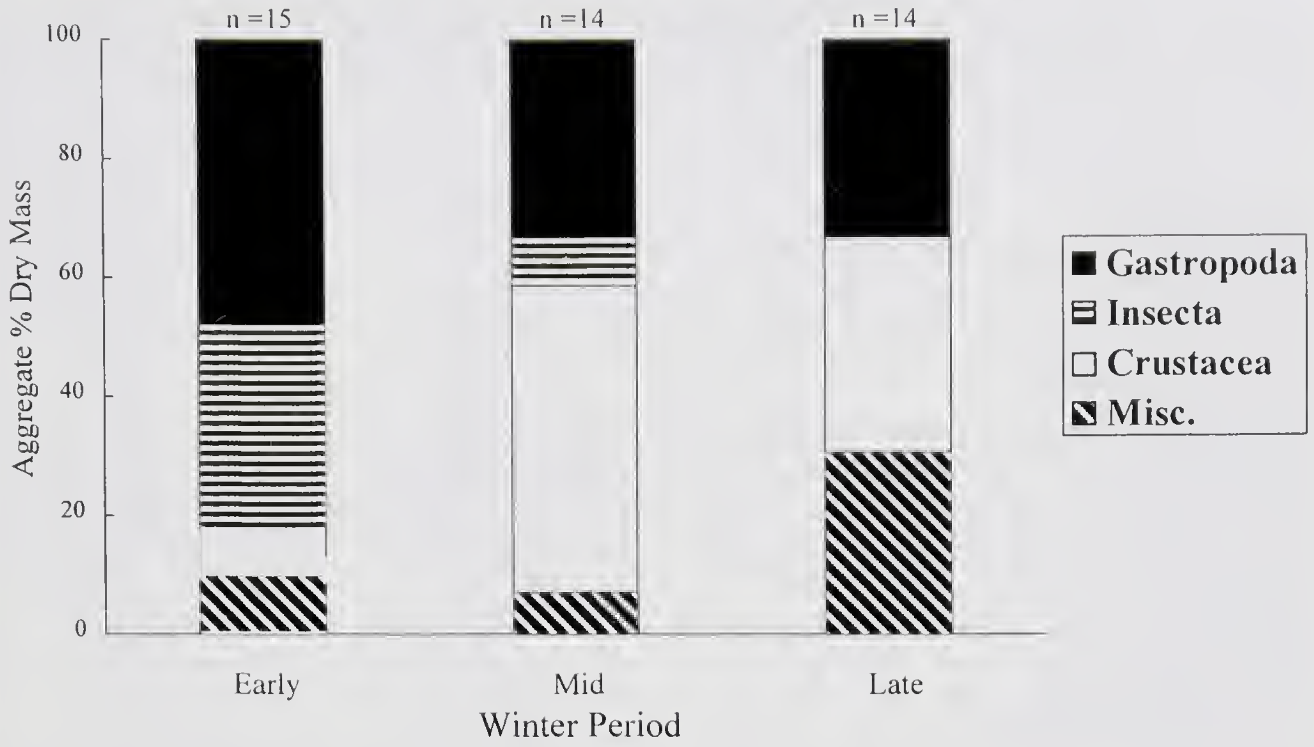

FIG. 3. Aggregate percent dry mass of diet classes identified from the upper digestive tracts of 43 Harlequin Ducks collected in winter at Shemya Island, Alaska, December 1995–March 1997.

pods), and dipterans (larvae and pupae), and did not vary between sexes ($Z = -0.46$, $P > 0.05$; $Z = 0.62$, $P > 0.05$; $Z = -0.67$, $P > 0.05$, respectively). Similarly, gross energy density of the diet was 11.38 (±0.75) kJ g^{-1} dry weight and did not differ by sex ($F_{1,39} = 0.06$, $P > 0.05$).

Food habits differed seasonally. Although consumption of crustaceans increased from early to midwinter ($\chi^2_2 = 8.00$, $P = 0.018$; Fig. 3), the opposite trend was detected for insect larvae ($\chi^2_2 = 6.54$, $P = 0.038$). Despite seasonal variation in the food habits of Harlequin Ducks, gross energy density of the diet did not differ between winter periods ($F_{2,39} = 0.48$, $P > 0.05$).

DISCUSSION

Our investigation of wintering Harlequin Ducks revealed how diurnal time budgets and food habits varied by sex, time of day, season, and environmental conditions. Although females spent more time feeding than males, both sexes fed longer in the evening, in midwinter, at high tide, and during shorter days. In contrast, neither diet composition nor gross energy density of the diet varied by sex. Diets changed during winter but gross energy density of the diet remained constant.

Different foraging strategies by each sex may reflect energetic and physiological constraints. For example, differences in body mass of Harlequin Ducks at Shemya Island (male: 750.9 ± 9.7 g, $n = 22$; female: 642.6 ± 8.7 g, $n = 23$) could explain why females fed more than males. Although total energy requirements increase with body size, smaller birds have higher metabolic costs per unit body mass (Calder 1974). Moreover, the larger ratio of surface area to body mass among smaller birds leads to more rapid heat loss (Calder and King 1974); thus female Harlequin Ducks may have to accumulate fat reserves more rapidly during the day than males to compensate for greater fat loss at night (Kendeigh et al. 1977). In addition, female nutritional requirements may exceed those of males because of fat requirements before egg production (Bergan et al. 1989).

Seasonally, the decrease in percent time feeding in late winter was likely caused by lengthening day length. In late winter, when days are longer, diurnal feeding birds may be able to satisfy their energy requirements using a smaller percentage of daylight time because the days are longer (Kendeigh et al. 1977).

Tidal patterns also influenced feeding behavior. The timing of feeding bouts may de-

TABLE 2. Aggregate percent dry mass and percent occurrence of prey items in the upper digestive tracts of 43 wintering Harlequin Ducks collected while feeding at Shemya Island, Alaska, December 1995–March 1997.

Species	Aggregate % dry mass	% occurrence
Buccinium baerii	2.16	11.63
Neptunea sp.	1.66	4.65
Littorina sitkana	21.39	34.88
Littorina sp.	2.57	4.65
Lacuna sp.	0.62	11.63
Margarites albolineatus	2.33	27.91
Cerithiopsis signa	0.05	2.33
Volutidae sp.	0.12	2.33
Mytilus edulis	0.18	2.33
Tectura sp.	1.73	4.65
Lottia digitalis	0.54	4.65
Lepidochitona sp.	0.07	2.33
Tonicella sp.	0.63	2.33
Schizoplax brandtii	3.74	27.91
Total Gastropoda	37.79	67.44
Anisogammurus locustoides	6.50	27.91
Anisogammurus pugittensis	3.34	11.63
Paramoera sp.	5.31	20.93
Halirages bungei	0.30	6.98
Melita sp.	0.21	6.98
Allorchestes malleolus	2.03	6.98
Ampithoe sp.	0.55	9.30
Parhyale ochotensis	1.51	6.98
Anonyx sp.	1.42	11.63
Pontogeneia sp.	1.89	13.95
Gammaridea sp.	0.76	39.53
Idotea fewkesi	0.19	9.30
Exoshaeroma sp.	0.42	6.98
Gnorimosphaeroma oregonensis	0.73	13.95
Pentidotea wosnesenskii	1.18	11.63
Pagurus aleuticus	1.30	2.33
Heptacarpus brevirostris	0.12	4.65
Hapalogaster grebnitzskii	0.36	4.65
Pugettia gracilis	3.07	9.30
Total Crustacea	31.17	76.74
Diptera pupae, *Brachycera* sp.	0.44	11.63
Diptera larvae, *Muscidae* sp.	13.72	13.95
Total Insecta	14.16	25.58
Cucumaria sp.	5.19	23.26
Total Holothuroidea	5.19	23.26
Strongylocentrotus droebachiensis	4.01	16.28
Total Echinoidea	4.01	16.28
Ulothrix sp.	3.70	4.65
Total Chlorophyta	3.70	4.65
Nereis sp.	0.37	4.65
Teribellidae sp.	0.99	2.33
Polychaete sp.	0.67	6.98
Total Polychaeta	2.04	13.90
Fish eggs	0.41	4.65
Cottidae sp.	0.04	2.33
Perciformes (*Stichaeidae* or *Pholidae*)	0.14	2.33
Stichaeidae sp.	0.19	2.33
Cyclopteridae sp.	0.10	2.33

TABLE 2. CONTINUED

Species	Aggregate % dry mass	% occurrence
Total Osteichthyes	0.88	11.63
Actinidae sp.	0.62	4.65
Total Anthozoa	0.62	4.65
Lepasterias sp.	0.16	4.65
Asteroidea sp.	0.28	2.33
Total Asteroidea	0.44	6.98

pend on the way tide affects the availability of food (Jorde and Owen 1988b). Harlequin Ducks fed on intertidal and subtidal prey but never above the waterline, despite the fact that gastropods were accessible and exposed at low tide. This behavior may explain why feeding was positively correlated with tide level. If Harlequin Ducks choose prey submerged or at the water's surface, then food availability will increase with rising tide. This explanation is consistent with foraging theory predicting that in environments with fluctuating food abundance, birds are predicted to allocate the greatest time in habitats with high food abundance and less in areas of low abundance (Pyke et al. 1977).

Harlequin Ducks at Shemya Island apparently were generalists that maintained a stable energy balance by substituting fly larvae for crustaceans as winter progressed and supplementing their diet with diverse prey items. The Harlequin Duck winter diet elsewhere in its range includes many food types typically dominated by gastropods and crustaceans (Kenyon 1961, Vermeer 1983, Goudie and Ankney 1986, Gaines and Fitzner 1987). While insects are an important food on the breeding grounds (Bengtson 1972), there are no published reports that fly larvae occur in the diets of Harlequin Ducks elsewhere during winter; thus, consumption of fly larvae might be an adaptation to the Aleutian environment.

Although Harlequin Ducks may be adaptable in their food habits, our results suggest that they are constrained in the amount of time they must spend feeding during the winter. Behavior of Harlequin Ducks is most restricted during midwinter when they spent 80% and 87% of the evening feeding (males and females, respectively). Given the large amount of time spent feeding during midwinter, Harlequin Ducks would not be able to extend their feeding bouts appreciably in the event of scarce food and or cold temperatures. Future research should examine the susceptibility of Harlequin Ducks to winter starvation. Also, researchers should determine if Harlequin Ducks are able to feed at night during periods of cold weather and food scarcity, identify seasonal fluctuations in food quality and availability, and determine the energetic costs of specific behaviors.

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HABITAT SAMPLING AND SELECTION BY FEMALE WILD TURKEYS DURING PREINCUBATION

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ABSTRACT.—Habitat use and home range sizes of female Eastern Wild Turkeys (*Meleagris gallopavo silvestris*) during preincubation may influence reproductive success. Little information on habitat selection during preincubation at multiple spatial scales is available and the influence of preincubation movement rates on reproductive success is poorly understood. We monitored 35 adult female Eastern Wild Turkeys during preincubation in central Mississippi during 1996–1997. We estimated home range and core area size, macrohabitat selection at multiple spatial scales and movement rates from 1 February until the beginning of incubation. Preincubation home ranges averaged 306.6 (±46.8 SE) ha and core areas 47.3 (±7.4) ha. Females selected 9–15 and 16–29 year-old pine (*Pinus* spp.) stands over other habitats available when establishing home ranges, but within these home ranges they selected pine stands that were older than 30 years for their core areas and nest sites. However, females used habitats within their established home range in proportion to availability. Movement rates averaged 286.5 (±22.3) m/hr during preincubation and were greater than during other seasons. We detected no correlations between home range or core area size and number of days nests were successfully incubated. However, we detected a positive correlation between movement rates and increased incubation, suggesting females that moved farther during preincubation successfully incubated nests longer. Our findings suggest females selected habitats differentially when establishing pre-incubation home ranges and core areas. Further, our findings suggest movement rates within home ranges may better reflect a female's habitat sampling effort during nest site selection rather than home range or core area size. *Received 17 Jan. 2000, accepted 10 April 2000.*

Reliable estimates of home range size are essential for understanding a species' behavioral ecology (Bekoff and Mech 1984). Areas of concentrated use within home ranges are often denoted as core areas (Kaufmann 1962), implying that these areas are preferred (Leuthold 1977). Non-migratory species should establish home ranges and select habitats that best meet their ecological requirements in the smallest possible space. Individuals should preferentially select portions of the landscape that enhance their survival and reproduction (Pulliam 1988). Specific to Eastern Wild Turkeys (*Meleagris gallopavo silvestris*), selection of suitable nest habitat, as determined by distribution of suitable nesting sites (Badyaev 1995), often requires extensive movement and increases in home range size relative to other activities (Badyaev et al. 1996a). Numerous researchers have examined seasonal home ranges in Wild Turkeys (e.g., Porter 1977, Smith et al. 1989, Kurzejeski and Lewis 1990); however, few have documented core area sizes, particularly during preincubation. Although home range size might influence reproductive success of Wild Turkeys (Badyaev et al. 1996a), the effect of variation of core area characteristics is unclear.

Habitat selection can influence survival and reproduction (Cody 1985, Badyaev et al. 1996b). During preincubation, female Wild Turkeys presumably shift habitat use to sample areas within their home range prior to nest initiation (Miller et al. 1999), assuming movements are not strongly influenced by interactions with other females or male display behaviors. Although Wild Turkey macrohabitat use has been extensively documented (Everett et al. 1985, Lambert et al. 1990, Speake et al. 1975, Wigley et al. 1986) and the need to examine habitat use at multiple spatial scales is recognized (Johnson 1980, Orians and Wittenberger 1991), little research has been directed towards Wild Turkey habitat selection at multiple spatial scales. Specifically, assessments of female habitat selection at multiple spatial scales during pre-incubation are scarce (Miller et al. 1999) and no study has examined selection processes at the core area level.

Variation in habitat quality across landscapes should favor individuals that select habitats providing the greatest reproductive

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success (Fretwell and Lucas 1970). In general, increased search time should increase the probability of selecting a better quality habitat (Stephens and Krebs 1986, Orians and Wittenberger 1991). Badyaev and coworkers (1996b) determined that increased habitat sampling (measured via preincubation range) allowed female Wild Turkeys to select higher quality nest sites, thereby increasing nest survival.

We evaluated spatial use characteristics, macrohabitat selection at multiple spatial scales, and movements during preincubation, and relationships among spatial use patterns, movements, and nest survival for female Wild Turkeys. Our objectives were to (1) examine spatial use characteristics (home range and core area sizes) during preincubation, (2) examine macrohabitat selection processes during preincubation at 3 spatial scales, (3) estimate seasonal movement rates, emphasizing movements during preincubation, and (4) assess relationships among spatial use patterns, movements, and nest survival for female Wild Turkeys in central Mississippi.

STUDY AREA AND METHODS

We conducted this research on the 14,410 ha Tallahala Wildlife Management Area (WMA), a 2,500-ha area owned by Georgia-Pacific Corporation and surrounding private lands in sections of Jasper, Newton, Scott, and Smith counties, Mississippi (89° 24′ N, 32° 15′ W. to 89° 04′ W 32° 05′ W). The Tallahala WMA contained 30% mature (>30 years old) bottomland hardwood [oak (*Quercus* spp.), hickory (*Carya* spp.)] forests, 37% mature pine (*Pinus taeda, P. echinata*) forests, 17% mixed pine-hardwood forests, and 11% in 1–15 year-old loblolly pine (*P. taeda*) plantations. The Georgia-Pacific area was adjacent to Tallahala WMA and was managed primarily for wood fiber production with 90% of the area comprised of 1–35 year-old loblolly pine plantations and the remaining 10% in Streamside Management Zones along creek drainages. Private lands were comprised mostly of mixed pine-hardwood and short-rotation pine forests. Topography was gently to moderately rolling, with 0–20% slope. Climate was mild, with a mean annual temperature of 20° C and mean annual precipitation of 152 cm.

We captured female Wild Turkeys with cannon nets on bait sites established during January–March 1996–1997 and July–August 1996. Capture sites were evenly distributed throughout the study area to ensure unbiased sampling of the population. Females were aged following Hewitt (1967). Captured adult females were tagged patagially (Knowlton et al. 1964), fitted with 85–100 g mortality sensitive radio-transmitters attached backpack style, and released at the capture site.

We located females by triangulation (White and Garrott 1990) using a hand-held 3-element Yagi antenna from predetermined telemetry stations ($n = 480$) at least five times/week. In most (98%) instances, distance from observer to female was within 1.0 km. We used two telemetry techniques to monitor females: systematic point and sequential locations. We obtained systematic point locations by recording two locations weekly for each female. We conducted sequential telemetry (focal runs) on a 4 hour basis with a location recorded on each female every hour for the entire 4 hour period. Azimuths for a single radio location were recorded within a 15 minute interval to reduce error caused by female movement; however, most (97%) consecutive azimuths were recorded within 7 min [$\bar{x} = 4.6$ min ± 0.02 (SE)]. Triangulation angles were maintained between 45° and 135° to reduce error and telemetry accuracy tests indicated that standard deviation from true bearing was 5.7°. Therefore, a circle circumscribing each female's location 1 km from each telemetry station would have an approximate area of 3.3 ha. Because the smallest macrohabitat patch on the study area was more than 5 ha and most (98%) locations were recorded within 1 km of each female, we assumed telemetry accuracy was sufficient for our analyses. To determine onset of incubation, hens located in the same location for two consecutive days were considered incubating, particularly when roosting did not occur.

Home range and core area analyses.—Female locations were entered into a dBASE III+ database and converted to a coordinate system using program TELEBASE (Wynn et al. 1990). We defined the preincubation season as 1 February to initiation of incubation. Home range (95%) and core area (50%) contour intervals were estimated using an adaptive kernel estimator in program CALHOME (Kie et al. 1994). Area observation curves conducted on five randomly chosen females indicated 32 locations were needed to estimate home range and core area sizes during preincubation. Therefore, we only estimated home ranges and core areas for females sampled with a minimum of 32 locations and for at least 75% of the preincubation season.

Movement rates.—We estimated movement rates (m/hr) by dividing the straight-line distance between sequential locations by the time interval. Only locations separated by less than 1.25 hours were used to ensure that distances between locations were associated with actual distances moved (Reynolds and Laundré 1990). We examined movement rates seasonally and considered the seasonal movement rate for each female as the experimental unit in analyses. To compare movement rates during preincubation to other seasons, we monitored females throughout the annual cycle and defined the remaining seasons as nesting (nest initiation–termination of nesting effort), brood-rearing (termination of nesting effort–30 September), and fall-winter (1 October–31 January). We used a one-way

ANOVA blocked by year to examine potential differences in movement rates across seasons and LSD multiple comparisons to test differences in mean separation of movement rates using SAS Version 6.12 (SAS Institute 1996). For home range, core area, and movement analyses, we tested homogeneity of variance using Levene's test (Milliken and Johnson 1992) and we used the Shapiro-Wilk statistic (Steel and Torrie 1980) to test for normality.

We used correlation analysis to test the hypothesis that female movement rates within preincubation home ranges were related to nest survival (days successfully incubated). Similarly, we used Pearson's correlation analysis to test the hypothesis that nest survival was related to preincubation home range or core area size.

Macrohabitat use.—We developed a Geographic Information System (GIS; ARC/INFO; ESRI, Redlands, California) with color infrared aerial photographs and 1:24,000 U.S. Geological Survey 7.5-min quadrangles. The U.S. Forest Service records from Bienville National Forest and stand data from Georgia-Pacific were used to classify stands into habitat types based on forest type (i.e., hardwood, pine) and stand age. We used year-specific stand maps and data to create two annual habitat coverages for the entire study area. We used aerial photographs, ground surveys, and landowner consultations to quantify habitat type on private lands within and surrounding the study area.

We delineated habitats as: mature (≥30 years) hardwood, mature mixed pine-hardwood, three classes of pine regeneration (0–8 years, 9–15 years, 16–29 years), mature pine (≥30 years), and other habitats (agricultural and Conservation Reserve Program lands ≤2 years old). Preincubation habitat use was investigated at 3 levels: (1) habitat use within home ranges versus availability of habitats across study area (first order), (2) habitat use in core areas versus availability of habitats within home range (second order), and (3) habitats used within home range versus availability of habitats in home range (third order). The outer boundary of our study area and study area habitat availability were determined using a buffer system around roads used for trapping Wild Turkeys during the study. We used the major axis length of the largest preincubation home range to buffer the road system in ARCVIEW (ESRI, Redlands, California). We estimated study area, home range, and core area habitat availability by summing the area for each habitat and dividing it by the total area of the study area, home range, or core area. We used compositional analysis (Aebischer et al. 1993) to examine pre-incubation habitat selection. After blocking by year, we tested differences of log-ratio habitat use and availability percentages with a multivariate analysis of variance (MANOVA) in SAS Version 6.12 for Windows 95 (SAS Institute 1996). We also calculated a mean rank for each habitat type within each scale of selection to provide an overall assessment of the importance of each habitat type. If significant differences were detected between habitat selection and availability at any scale, a ranking matrix of t-tests was constructed to examine order of selected habitat (Aebischer et al. 1993).

Nest survival and success.—After 5 days of incubation, nests were approached to within 50 m and azimuths were taken towards the nest from several points around it. After cessation of nesting activity, nests were located using marked reference points to determine nest fate. We calculated nest survival by recording the number of days females successfully incubated nests prior to nest loss or hatch. We defined nesting success rate as the proportion of hens initiating incubation that successfully hatched at least 1 egg.

RESULTS

We monitored 2319 locations of 35 females to estimate home range, core area size, macrohabitat use, and movement rates during preincubation. We monitored 2600 locations of incubating females. Thirty-three females were relocated enough times to estimate home ranges and assess habitat selection. Two females could not be monitored intensively because of radiotransmitter failure midway through the preincubation period. Number of relocations/female averaged 58 during preincubation. Home range and core area sizes averaged 306.6 (±46.8) ha and 47.3 (±7.4) ha, respectively.

Macrohabitat use.—Differences in use and availability differed at first order selection ($F_{6,31} = 7.5$, $P < 0.001$), indicating females used habitats different from availability of habitats across the study area, selecting 9–29 year old pine stands over other habitats (Table 1). Differences in use and availability also differed at second order selection ($F_{6,31} = 3.88$, $P = 0.005$), indicating females used habitats at the core area level different from the availability of habitats within the home range. Females selected mature pine stands over other habitats. However, differences in use and availability were not different at third order selection ($F_{6,25} = 0.55$, $P > 0.05$), indicating females used habitats within home ranges similar to the proportion of those habitats.

Nest survival and success.—Nest initiation rates averaged 73% during 1996 and 87% during 1997. Only 2 females renested during this study; neither was successful. Estimates of nest survival averaged 14.2 days and nest success averaged 10%.

Movement rates.—Movement rates differed across seasons ($F_{3,108} = 14.83$, $P < 0.001$). Females moved at greater rates during prein-

TABLE 1. Mean ranks (1 = least, 7 = greatest) of habitat use across 3 spatial scales based on compositional analysis for adult female Eastern Wild Turkeys during preincubation on Tallahala Wildlife Management Area, Georgia-Pacific Corporation, and surrounding private lands, Mississippi, 1996–1997.

Habitat type	Order of habitat selection[a]			Overall
	1st	2nd	3rd	
Mature hardwood (≥30-yr-old)	1	6	5	4.0
Mature mixed pine-hardwood (≥30-yr-old)	5	3	3	3.7
Pine (0–8-yr-old)	3	1	1	1.7
Pine (9–15-yr-old)	6	2	2	3.3
Pine (16–29-yr-old)	7	5	6	6.0
Mature pine (≥30-yr-old)	2	7	7	5.3
Other (agricultural areas, openings)	4	4	4	4.0

[a] 1st order—habitat selection across home range versus availability of habitats across study area; 2nd order—habitat selection in core areas versus availability of habitats within home ranges; 3rd order—habitats used within home range versus availability of habitats in home range.

cubation ($\bar{x}$ = 286.5 m/hr ± 22.3) than during brood-rearing (only non-brooding females; $\bar{x}$ = 201.3 m/hr ± 10.6), fall-winter ($\bar{x}$ = 198.7 m/hr ± 40.1), or nesting ($\bar{x}$ = 122.8 m/hr ± 15.4).

Relationships between spatial use patterns, movements, and nest survival.—We did not detect correlations between preincubation home range size ($r = 0.216$, $P > 0.05$, $n = 21$) or core area size ($r = 0.124$, $P > 0.05$, $n = 21$) and duration of nest survival. However, duration of nest survival was positively correlated to preincubation movement rates ($r = 0.468$, $P = 0.037$, $n = 21$).

DISCUSSION

Variability in habitat quality should favor individuals choosing habitats producing greater survival and reproductive success (Fretwell and Lucas 1970). Habitat sampling (i.e., movements) by females during preincubation should decrease with increasing habitat quality or decreased variability (Stephens and Krebs 1986). In turn, female movements (i.e., habitat sampling) could be influenced by the spatial distribution of resources, experience or age, or perhaps physiological condition of the female. Renesting effort on the study area is considerably lower than in other areas of Eastern Wild Turkey range (Miller et al. 1998, this study); thus, initial nesting efforts constitute the majority of reproductive efforts for this population. Therefore, reproduction on our study area is temporally limited in that females usually invest considerable resources into only a single clutch. Because females should preferentially select portions of the landscape optimizing reproductive potential (Fretwell and Lucas 1970), we predicted females would exhibit greatest habitat sampling prior to nest initiation, presumably to locate a nest site that increased probability of nest survival. Our findings supported this prediction, because female movement rates were greatest during preincubation compared to other seasons. However, female home ranges were not seasonally largest during preincubation (Chamberlain 1999), suggesting that females did not necessarily increase the portion of the landscape they sampled but rather intensified sampling efforts within established home ranges prior to nest initiation.

Females selected 9–29 year-old pine stands at the home range level, but selected mature pine stands at the core area level. Additionally, mature hardwood stands were consistently ranked higher than other habitat types, except mature pine, at the core area scale of selection. Selection of mature pine stands likely resulted from an increased availability of quality nest sites because microhabitat characteristics in mature pine stands were desirable for nesting (Chamberlain and Leopold 1998). Most nest attempts on the study area occurred in mature pine stands or pine regeneration areas (Miller et al. 1999) and nesting success was greatest in mature pine stands compared to other available habitats (Seiss et al. 1990). Many mature pine stands were intensively managed (i.e., thinned and prescribe burned) for Red-cockaded Woodpeckers (*Picoides borealis*) during our study. These stands contain more herbaceous vegetation, a key component of nest sites on our study area, relative to other stands (Palmer et al. 1996). Pine stands receiving prescribed fire on a 2–4 year rotation also provided quality brood-rearing habitat (Phalen et al. 1986). Therefore, females selecting mature pine stands within core areas during preincubation are reproductively adaptive, both for nesting and brood-rearing.

Females used habitats similar to their availabilities within their home range. Our findings suggest females selected home ranges and core areas based on a defined proportion of habitats, but sampled those habitats similar to availability within these areas, suggesting the use of multiple scales of selection during preincubation. The nondifferential use of habitats within home ranges also suggests females distribute sampling intensity across habitats within their home range, presumably to locate a nest site with a particular suite of habitat characteristics.

Badyaev and coworkers (1996b) and Miller and coworkers (1999) indicated successful females used areas within their home range differently than unsuccessful females. Regrettably, nest success in this study was very low, and given the large proportion of unsuccessful females in our marked population, examining potential differences in habitat selection between successful and unsuccessful females was not possible. We encourage other researchers to examine relationships between habitat sampling and reproductive success in other areas of Eastern Wild Turkey range.

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DIURNAL ROOST SITE CHARACTERISTICS OF NORTHERN SAW-WHET OWLS WINTERING AT ASSATEAGUE ISLAND, MARYLAND

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ABSTRACT.—We characterized 30 diurnal roost sites of five radio-tagged Northern Saw-whet Owls (*Aegolius acadicus*) in the winters of 1996–1997 on Assateague Island, Maryland and found they preferred thick cover at roost sites. Roosts occurred most often in loblolly pine forest (*Pinus taeda*) and shrub swamps dominated by wax myrtle (*Myrica cerifera*). Vegetation was measured at paired roosts and random sites in similar habitats. Distance to nearest tree and average canopy height were significantly lower at roost sites than random sites. Numbers of stems larger than 2.5 cm diameter at breast height (dbh), stems smaller than 2.5 cm dbh, and roost tree dbh were larger at roost sites. Roost height, canopy cover, canopy height, shrub height, and ground cover differed significantly between pine and shrub swamp roosts, although cover above and below the roost site were similar. Higher densities of stems and shorter distances to the nearest tree at roost sites compared to random sites indicated that owls chose sites with dense cover, probably as protection from predators or weather. *Received 22 June 1999, accepted 18 March 2000.*

Several researchers have examined Northern Saw-whet Owl (*Aegolius acadicus*) diurnal roost site characteristics (Randle and Austing 1952; Hayward and Garton 1984; Grove 1985; Swengel and Swengel 1987, 1992) but not on a coastal barrier island. The coastal shrub community encompassing both pine forest and shrub swamp is a unique environment that may provide important wintering habitat for Northern Saw-whet Owls (Loos and Kerlinger 1993). The barrier island flora includes many plant species missing from inland habitats and the vegetation structure is very different from that of most inland plant communities in the eastern United States (Hill 1986).

Knowledge of diurnal roost site characteristics of Northern Saw-whet Owls may lead to a better understanding of their habitat requirements and help researchers evaluate the suitability of an area to support owls. The contrast between coastal and inland Northern Saw-whet Owl habitats and the lack of information on this issue prompted this study. Specifically, in an attempt to determine which variables are important to roosting owls, we compared vegetation characteristics at roost sites and random sites, and between pine forest and shrub swamps.

STUDY AREA AND METHODS

Assateague Island is a narrow coastal barrier island of approximately 7252 ha located in Worcester County, Maryland and Accomack County, Virginia (Hill 1986). Its northernmost point is at the south end of the Ocean City Inlet, Ocean City, Maryland. The 1621 ha study area was located within Assateague Island National Seashore (38° 10′ N, 75° 10′ W). The study area consisted of tidal marsh (36.1%), shrub swamp (35.7%), loblolly pine (*Pinus taeda*) forest (6.9%), and deciduous forest (1.4%), with some grassland (10.0%) and beach (8.6%) on the eastern side of the island (Churchill 1998). Open water made up the remaining 1.3%. Northern Saw-whet Owl roosting habitat occurred primarily in the shrubland and forested areas with few suitable perches in other areas.

We characterized one Northern Saw-whet Owl dayroost site used by a single owl at Assateague Island in February, 1996 and 29 sites used by four owls from December, 1996 to March, 1997. Roosts were located by radio-tracking owls (Churchill. 1998) fitted with 3 g backpack transmitters (model sopb 2070 mvs from Wildlife Materials Inc., Carbondale, Illinois). Sites were then flagged so they could be relocated and characterized after the owls left. Vegetation and roost site characteristics were measured in a 3 m radius circular plot centered on the roost tree. The following variables were measured: number of stems less than 2.5 cm diameter at breast height (dbh), number of stems 2.5–8 cm dbh, roost tree height, percent canopy cover (3 measurements equally spaced along each quadrant boundary line for a total of 12 measurements within the 3 m plot), a visual estimate of average canopy height and average shrub height, roost tree dbh, distance to nearest tree (>8.0 cm dbh) within 6 m, and an estimate of percent ground cover (shrubs/forbs,

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TABLE 1. Vegetation of Northern Saw-whet Owl roosts on Assateague Island, Maryland, 1996–1997.

Owl ID[a]	Roost site frequency Loblolly pine	Shrub swamp[b]	Other
150.178	4 (4 obs.)[c]	8 (8 obs.)	1 (1 obs.)[d]
150.217	6 (26 obs.)	0	1 (1 obs.)[e]
150.247	8 (8 obs.)	0	1 (2 obs.)[f]
150.338	0	1 (1 obs.)	0
150.188	1 (1 obs.)	0	0
Total	19 (39 obs.)	9 (9 obs.)	3 (4 obs.)

[a] Owl ID represents the frequency of the attached transmitter (in MHZ).
[b] Roosts in wax myrtle (*Myrica cerifera*).
[c] Number of observations (obs.) indicates that owls were observed in the same roosts more than once.
[d] Multiflora rose (*Rosa multiflora*).
[e] Red maple (*Acer rubrum*).
[f] Red cedar (*Juniperus virginiana*; not measured).

leaves, sticks, and other; Churchill 1998). Trees beyond 6 m were assumed to have little or no effect on the immediate roost environment. The same variables were measured at a random site in the same habitat as the roost. The random site was centered around a tree that was located 30 m away in a random direction from the roost. Variables measured at roost sites that did not apply to random sites were roost height, distance perched from trunk, concealment cover above and below the roost, and orientation of the roost branch.

We used Wald's χ^2 statistic from stepwise logistic regression (Hosmer and Lemeshow 1989; entry level = 0.15; stay level = 0.10; PROC LOGISTIC in SAS v. 6.12 for Windows; SAS Institute Inc. 1989) to determine which habitat characteristics differentiated between roost and random sites. The initial model included 12 variables: tree height, canopy cover, average canopy height, average shrub height, roost tree dbh, number of stems less than 2.5 cm, number of stems greater than 2.5 cm, distance to nearest tree, and four categories of ground cover (shrub, leaves, sticks, and other). The "other" category consisted of grass (65%) and water (close to 35%). If no tree occurred within 6 m of the roost tree, a default value of 7 m was used for distance to the nearest tree. Because of small sample sizes, we used Wilcoxon rank sums, a non-parametric statistic that accounts for small sample sizes (Hollander and Wolfe 1973) to compare characteristics of roosts used by owls in pine forest (n = 19) and shrub swamp (n = 9). Roost orientation was calculated for circular distributions after Zar (1999).

RESULTS

Nineteen of 31 roosts were in pine forest (Table 1), although two different roosts used by one owl occurred in the same tree making a total of 30 different roost sites. Roost sites rarely occurred outside of the loblolly pine forest or shrub swamp habitats. Three of the five owls were located at more than one roost.

Five variables distinguished roosts from random sites (Table 2). Roost sites had more large stems (greater than 2.5 cm dbh; Wald's χ^2 = 6.63, 29 df, P = 0.01) and more small stems (less than 2.5 cm dbh; Wald's χ^2 = 4.09, 29 df, P = 0.04) than random sites. Tree diameters were larger at roost sites (Wald's χ^2 = 4.69, 29 df, P = 0.03). Distance to nearest tree was shorter (Wald's χ^2 = 5.97, 29 df, P = 0.02) and average canopy height lower (Wald's χ^2 = 6.42, 29 df, P = 0.01) at roost sites than random sites. Roost orientation was not significant at pine roosts (n = 19, r = 0.39, $P > 0.05$), shrub swamp roosts (n = 9, r = 0.09, $P > 0.05$), or combined roosts (n = 31, r = 0.30, $P < 0.05$).

Roost sites in pine forest and shrub swamp roost sites differed for 10 of the 17 variables we compared (Table 2). Average roost height was significantly lower in shrub swamp areas [1.0 ± 0.2 m (SE)] than in pine forest (4.0 ± 0.8 m; $Z = -3.20$, 8 df, P = 0.001), possibly because the lower roost tree height in shrub swamp areas (2.9 ± 0.3 m) than in pine forest (7.9 ± 0.7 m; $Z = -3.59$, 8 df, P = 0.003; Table 2). Number of stems smaller than 2.5 cm averaged higher (289 ± 95) at shrub swamp sites than at pine roost sites (143 ± 54; $Z = -2.12$, 8 df, P = 0.03; Table 2). Two variables of note that did not differ between pine forest and shrub swamp roosts were concealment cover above ($Z = -0.84$, 8 df, $P > 0.05$) and below (Z = 0.32, 8 df, $P > 0.05$) the roost.

DISCUSSION

We expected to find Northern Saw-whet Owls roosting in pines on Assateague Island because conifers were often reported as roost trees for Northern Saw-whet Owls (Randle and Austing 1952; Hayward and Garton 1984; Grove 1985; Swengel and Swengel 1987, 1992). Most owls in our study roosted in pines, even though pine woods represented only 6.7% of the study area (Churchill 1998). The use of shrub swamp roost sites on Assateague Island exemplifies the uniqueness of the coastal barrier island as Northern Saw-whet Owl habitat. In our study, 39% of roosts were not in pines. These areas probably would not have been searched if owls had not been detected there

TABLE 2. Characteristics of shrub swamp and pine Northern Saw-whet Owl roosts at Assateague Island, Maryland, 1996–1997.

	Shrub swamp ($n = 9$)		Pine forest ($n = 19$)		Combined ($n = 28$)		Random ($n = 28$)	
Variable	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Roost height (m)[a]	1.0	(0.5–2.0)	4.0	(0.8–10.7)	2.9	(0.5–10.7)	—	—
Roost orientation (degrees)	166	(0–349)	158	(10–265)	168	(0–349)	—	—
Distance to trunk (cm)	64	(0–290)	152	(0–460)	116	(0–460)	—	—
Roost tree height (m)[a]	2.9	(1.9–4.8)	7.9	(2.0–12.3)	6.1	(1.1–12.3)	6.7	(1.1–14.0)
Above cover (%)	50	(5–85)	50	(10–95)	51	(5–95)	—	—
Below cover (%)	30	(5–65)	20	(5–95)	24	(5–95)	—	—
Canopy cover (%)[a]	0	(0–33)	60	(0–100)	39	(0–100)	41	(0–92)
Average canopy height (m)[a,b]	2.4	(0–7.6)	7.6	(0–11.1)	6.1	(0–11.1)	7.0	(0–14)
Average shrub height (cm)[a]	305	(200–396)	217	(100–300)	247	(100–396)	244	(60–460)
Roost tree dbh (cm)[a,b]	4	(2–7)	25	(3–45)	18	(2–45)	16	(1–42)
Nearest tree (m)[a,b]	6.2	(3.3–7.0)	3.6	(2.0–7.0)	4.4	(2.0–7.0)	4.7	(1.8–7.0)
Number of stems <2.5 cm dbh[a,b]	289	(56–847)	143	(2–978)	183	(2–978)	58	(0–254)
Number of stems >2.5 cm dbh[b]	7	(0–18)	3	(0–15)	5	(0–18)	2	(0–11)
Ground cover (%)								
Shrub/forbs	0	(0–24)	10	(0–34)	7	(0–34)	5	(0–16)
Leaves/pine needles	50	(0–100)	80	(20–98)	64	(0–100)	57	(0–91)
Sticks[a]	0	(0–9)	10	(0–18)	6	(0–18)	7	(0–28)
Other[a,c]	50	(0–93)	10	(0–80)	25	(0–93)	32	(0–95)

[a] Pine and shrub swamp roost sites were significantly different at $P \leq 0.05$ using Wilcoxon rank sum tests for small sample size.

[b] Roost and random sites were significantly different at $P \leq 0.05$ using Logistic Regression.

[c] The "other" category of ground cover consisted of water, sand, and grass.

via telemetry because they often occurred where thick vegetation hindered accessibility. Consequently, other methods of locating owls (and subsequent roost site characterization) such as visual detection of roost sites, could be biased by the relative ease of locating roosts in conifers. Only three of five published roost site studies (Randle and Austing 1952, Hayward and Garton 1984, Grove 1985) described roosts in trees other than pines and in each case, such roosts were uncommon.

Average roost tree height and diameter were much greater in Idaho (Hayward and Garton 1984) while average roost tree height in Wisconsin (Swengel and Swengel 1992) was slightly greater than at Assateague Island (Table 3). The shorter roost trees in Maryland may be due to several factors including stunted growth of loblolly pines caused by the harsh coastal environment, species differences between the loblolly pines at Assateague Island and pine species found in Wisconsin and Idaho, or the lack of roosts other than pines in other studies. The range in height of the roost itself was relatively similar in all studies except ours (Table 3). Roost height may be influenced by the risk of predation as has been suggested for Eastern Screech-Owls (*Otus asio;* Duguay et al. 1997).

In several studies, including ours, owls often roosted far from the trunk (Table 3). This distal positioning on the branch is possible for a small lightweight owl, whereas the ends of the branch would not support a larger, heavier bird. Grove (1985:23) described Northern Saw-whet Owl roosts as being far from the main trunk "where cover density was greatest".

Because Northern Saw-whet Owl roost sites have been documented in a variety of habitats, roosts in shrub swamp areas were not unexpected. Pine forest may be preferred over shrub swamp, but our results suggest owls roost wherever cover is dense. Northern Saw-

TABLE 3. A comparison of Northern Saw-whet Owl roost site characteristics.

Characteristics	Idaho[a] (3 owls) (range, *n* roosts)	Ohio[b] (NA owls)[h] (range, *n* roosts)	Maryland[c] (5 owls) (range, *n* roosts)	Washington[d] (NA owls) (range, *n* roosts)	Wisconsin[e] (NA owls) (range, *n* roosts)	Wisconsin[f] (NA owls) (range, *n* roosts)
Roost tree height	22.6 ± 3.04 m (—, 15)	—[h]	6.1 ± 3.5 m (1.1–12.3 m, 30)	—	—	9.2 ± 3.4 (1.5–22 m, 591)
Roost tree dbh	46.0 ± 8.2 m (—, 15)	—	17.4 ± 13.4 cm (2.0–45.0 cm, 30)	—	—	15.9 ± 6.3 cm (1–48 cm, 472)
Perch height	4.2 ± 0.6 m (0.9–7.3 m, 15)	usually 2.4–3.0 m (max 5.5 m, 15)	2.9 ± 3.0 m (0.5–10.7 m, 30)	— (0.7–7.7 m, 90)	— (0.69–7.67 m, 90)	4.1 ± 2.2 m (0.15–11.2 m, 429)
Perch distance	—	— (50–75% BL,[g] 15)	119.7 ± 132.6 cm (0–460.0 cm, 30)	— (30–183 cm, 8)	—	30.9 ± 22.2% BL (1.3–100% BL, 372)

[a] Hayward and Garton 1984.
[b] Randle and Austing 1952.
[c] Churchill 1998.
[d] Grove 1985.
[e] Swengel and Swengel 1987.
[f] Swengel and Swengel 1992.
[g] BL = branch length.
[h] Information not available.

whet Owls roosted in areas with high stem densities. Roost sites with the highest stem densities often were in wax myrtles within shrub swamps where the stems were predominantly common reeds (*Phragmites australis*) over 2 m tall. Roost sites in pine forests often had high densities of greenbriar (*Smilax* spp.). The greenbriar was so dense at one red cedar *(Juniperus virginiana)* roost, we could not measure the roost characteristics. Judging by our difficulty of finding some of these roosts from the ground, common reeds and greenbriar may provide excellent cover from terrestrial predators. Concealment cover above roosts was the same (50%) for both shrub swamp and pine forest roosts suggesting that owls key in on cover in roost selection rather than selecting for specific plant species.

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GEOGRAPHIC VARIATION AND TAXONOMY OF THE NORTHERN WATERTHRUSH

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ABSTRACT.—In this study we analyzed geographic variation in the Northern Waterthrush (*Seiurus noveboracensis*) and reassessed the status of the four subspecies described between 1880 and 1948, three of which were recognized by the AOU Check-list (1957) and Godfrey (1986). We examined 490 specimens that came from throughout the breeding range of the Northern Waterthrush and used four morphometric data sets and three color variables to investigate geographic variation. Males differed from females based on morphometric characters. Males, unlike females, showed a morphometric trend with latitude and longitude. Their wing chord, tail and tarsus lengths showed a gradual decrease in length from north to south, while their tail and tarsus lengths gradually decreased eastward. The body shape showed a longitudinal trend where western specimens tended to have proportionally longer tails than wings compared to specimens from the eastern part of the range. Color was more strongly related to geography than morphometric characters and showed both longitudinal and latitudinal trends. Specimens from the southeastern part of the range were more olive dorsally and yellow ventrally and had fewer underpart markings than most specimens from the northwestern part of the range. Only the wing length permitted us to discriminate between the most distant populations. These trends are clinal and cannot support the recognition of subspecies. *Received 5 July 1999, accepted 4 March 2000.*

The breeding range of the Northern Waterthrush (*Seiurus noveboracensis*) extends along tree line from Alaska to Newfoundland and south to the northern part of the United States (Godfrey 1986, AOU 1998). Differences between populations have been primarily based on color variation and, to a lesser extent, on morphometric distinctions. Ridgway (1880, 1902) divided the species into two subspecies, *S. n. notabilis,* ranging from northwestern Alaska to western Quebec, and *S. n. noveboracensis,* ranging from western Quebec to Newfoundland. The western form was similar to the eastern subspecies, but had a larger bill, whiter ventral coloration, and more grayish olive dorsal coloration. McCabe and Miller (1933) proposed a third subspecies, *S. n. limnaeus,* restricted to northwestern and central British Columbia that represented an intermediate form with a darker dorsal coloration, olivaceous black to dark grayish olive, and yellowish ventral coloration, paler than *S. n. noveboracensis* but darker than *S. n. notabilis.* Its bill, wing, and tail lengths were smaller than those of the other subspecies but its tarsus was similar to *S. n. notabilis* (McCabe and Miller 1933). A fourth subspecies, *S. n. uliginosus* (Burleigh and Peters 1948), was described as olivaceous dorsally and yellowish ventrally with longer wing and tail than those of the other populations. Its breeding range was restricted to the islands of Newfoundland, Saint-Pierre, and Miquelon. The geographical distribution of the four subspecies on their breeding range, based on Burleigh and Peters (1948), AOU (1957), and Godfrey (1986) is given in Fig. 1.

Eaton (1957) concluded that the Northern Waterthrush was monotypic and believed that geographic variation indicated only geographic trends. Todd (1940) originally recognized the validity of the subspecies but later supported Eaton's conclusions (Todd 1963). No other studies have addressed the status of the Northern Waterthrush subspecies or geographic variation within this species.

Eaton's (1957) and Todd's (1963) papers appeared too late to be taken into account for the AOU (1957) Check-list, which continued the broad use of the subspecies recognized at that time (Gabrielson 1959, Godfrey 1986). The disagreement over the validity of subspecies in *Seiurus noveboracensis* (AOU 1957 vs Eaton 1957) led us to re-examine geographic variation in this species. Our goal was to review variation patterns and to assess the taxonomic status of the known subspecies. Availability of new specimens in museum collec-

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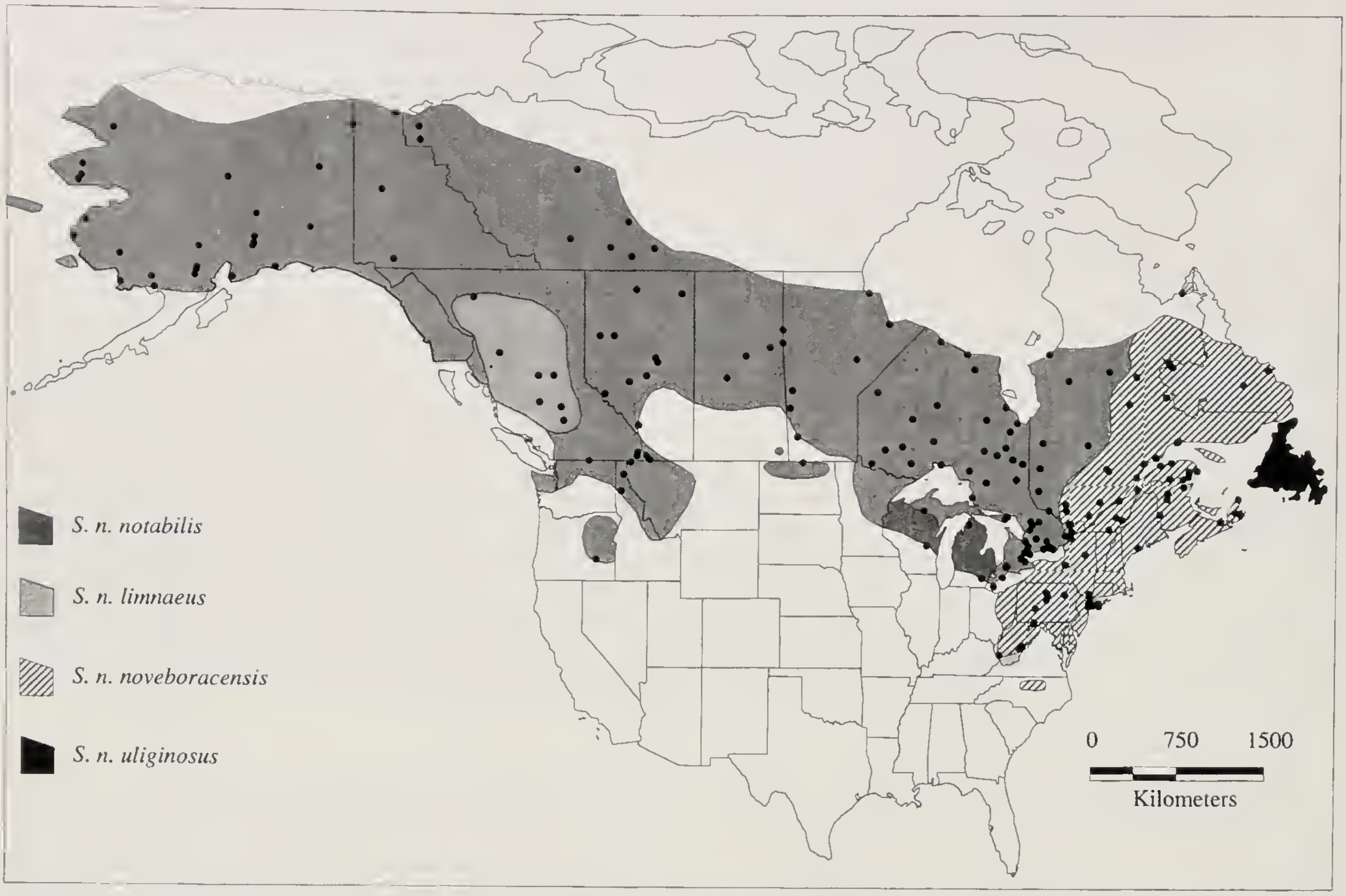


FIG. 1. Breeding range of the four subspecies of the Northern Waterthrush (Burleigh and Peters 1948, AOU 1957, Godfrey 1986). Dots correspond to the locations of the 490 specimens used in this study.

tions and more sensitive statistical analyses provided the basis for our study.

METHODS

We examined 556 museum specimens, but data from only 490 (329 males and 161 females) were analyzed. To minimize variation caused by sex, age, or season, juveniles and birds with worn or broken feathers were excluded. Furthermore, only adults taken on the breeding range and during the breeding season (May 15 to July 31) were analyzed. We included samples from the entire breeding range (Fig. 1).

Sex, age, date of collection, and locality were obtained from specimen labels. Buffy tipped tertials and/or pointed rectrices were used to identify immature specimens. When no geographical coordinates were available from the labels, we obtained the information from the web sites of the Geographic Names Information System of the U.S. Geological Survey, U.S. Department of the Interior (http://www.nmd.usgs.gov/www/gnis/gnisform.html) and Geomatics Canada, Natural Resources Canada (http://Geonames.NRCan.gc.ca/english/cgndb.html).

We measured four characters with dial calipers (±0.1 mm) on all specimens: (1) unflattened wing chord, from bend of wing to longest primary; (2) tail length, from point of insertion to tip of longest rectrix; (3) bill length from a nostril to tip; and (4) tarsus length.

Plumage coloration was assessed under natural light on sunny days or under artificial overhead lighting. The colors of three areas were recorded: dorsal coloration, ventral coloration, and underpart markings (breast streaks). Each area was divided into classes and was scored on that basis. The scoring of each color class was made by studying the 221 specimen that came from the Canadian Museum of Nature and by identifying the specimens that best represented the different color trends of that sample. Those specimens were kept as standards when we assessed the color classes at other museums. The color classes were given the following numerical values: dorsal coloration: 1 for dark brown, 2 for olivaceous brown, and 3 for olive; the ventral coloration: 1 for white, 2 for yellowish, 3 for yellow, and 4 for intense yellow; and the underparts: 1 for few markings, 2 for intermediate amount, and 3 for densely marked.

We tested sexual dimorphism for both morphometric and coloration variables with the Kruskal-Wallis test (Sokal and Rohlf 1981).

Geographic variation.—We examined the relationships between morphometric and geographic variables using a principal component analysis (PCA; Jolicoeur and Mosimann 1960). The centered PCA performed on the covariance matrix was found to be the most efficient method. Principal component axis one (PC1) was interpreted as the size components and axis 2 (PC2) was considered an indicator of body shape (Jolicoeur and Mosimann 1960, Yoccoz 1993). The size variable described the magnitude of a given character, whereas shape was estimated by the relationship between two or more characters (e.g., the wing becoming larger when the tail shortens; Jolicoeur and Mosimann 1960, Somers 1986). Because previous studies on the Northern Waterthrush used techniques that did not differentiate between size and shape (Ridgway 1902, McCabe and Miller 1933, Burleigh and Peters 1948), we used both components for analyzing geographic variation patterns. Regressions of PCA scores against latitude and longitude were made to analyze geographic variation in size and shape.

Color data were analyzed by multiple correspondence analysis (MCA). The multiple correspondence analysis of qualitative color variables is equivalent to normalized PCA of quantitative variables (Tenenhaus and Young 1985). As for the morphological analyses, regression of the components against latitude and longitude was calculated and one-tailed tests of significance (F-test) were computed for regression coefficients.

Maps with isocontours were used to display geographic variation over the breeding range. Calculations for PCA, MCA, and contour curves were made with the ADE-4 (1997) software, version 1997 for Windows 95 (Chessel et al. 1996, Thioulouse et al. 1997).

Size and color differences.—The specimens were separated into four groups based on the known breeding distribution of the four subspecies (Burleigh and Peters 1948, AOU 1957, Godfrey 1986; see Fig. 1). The Kruskal-Wallis test, done with Statistix (1996) version 1.0 for Windows 95, was used to indicate which of the described subspecies could be differentiated by the morphological and color variables.

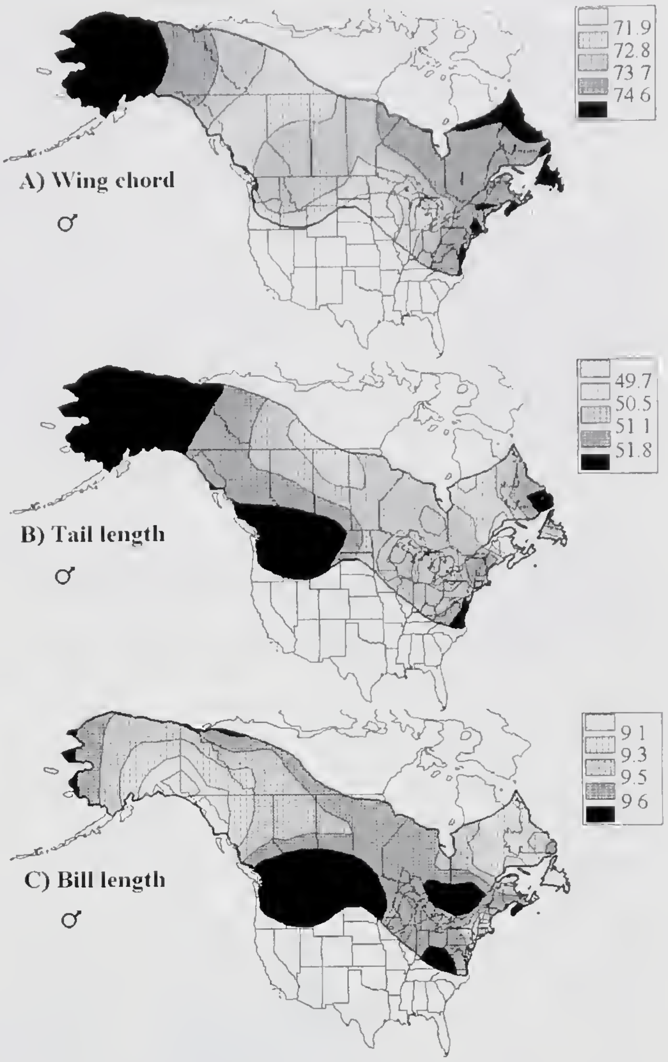


FIG. 2. Isocontours for (A) wing chord, (B) tail and (C) bill lengths in male Northern Waterthrushes based on their breeding distribution. The legends on the right indicate the limit values between isocontour shades.

RESULTS

Sexual dimorphism.—The four morphometric measurements (wing: $F = 107.86$, 1 df, $P < 0.001$; tail: $F = 66.34$, 1 df, $P < 0.001$; bill: $F = 45.34$, 1 df, $P < 0.001$; tarsus: $F = 7.43$, 1 df, $P < 0.0066$) showed a significant difference between sexes. In addition, females had dorsal color more olivaceous than males ($F = 36.42$, 1 df, $P < 0.001$). As a consequence, all subsequent analyses of size and color parameters were performed separately for each sex.

Geographic variation.—Wing chord, tail and tarsus lengths of males were positively correlated with latitude, but bill length was negatively correlated (Fig. 2A–C, Table 1). Tarsus length and tail length were correlated with longitude, but not bill length or wing chord (Table 1). Tail length showed the strongest relationship with latitude (Table 1; Tail = 49.422 + 0.069 × Lat.) and longitude (Table 1; Tail = 51.104 + 0.02 × Long.). No significant relationship was found for females between morphometrics and geographic location, except for tarsus, which was positively correlated with longitude (Table 1).

The dorsal and ventral coloration of both sexes varied with latitude and longitude (Table 1). In males, the yellowish coloration of the breast and the olivaceous color of the dorsal region both increased in the southeastern portion of the range. Females from the northwestern parts of the range had heavier markings on their undersides than those from the east (Table 1).

Males showed significant relationships between the size (PC1) component and both with latitude and longitude (Table 2). They showed similar relationships between the

TABLE 1. Coefficient of correlation (*r*) and *P* values from regression of morphometric and color variables with longitude and latitude in male and female Northern Waterthrushes.

	Latitude				Longitude			
	Males[a]		Females[a]		Males[a]		Females[a]	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Morphometric variables								
Wing chord	0.139	0.01	0.013	>0.05	0.023	>0.05	−0.122	>0.05
Tail length	0.235	<0.001	−0.016	>0.05	0.281	<0.001	0.028	>0.05
Bill length	−0.155	0.005	0.036	>0.05	−0.003	>0.05	0.122	>0.05
Tarsus length	0.118	0.031	0.139	>0.05	0.172	0.002	0.203	0.01
Color variables[b]								
Dorsal color	−0.208	<0.001	−0.135	>0.05	−0.212	<0.001	−0.257	0.001
Ventral color	−0.187	<0.001	−0.389	<0.001	−0.376	<0.001	−0.507	<0.001
Underpart markings	−0.081	>0.05	0.231	0.003	0.013	>0.05	0.224	0.004

[a] df = 327 for males, 159 for females.

[b] Numerical values of color classes: dorsal color: 1 for dark brown, 2 for olivaceous brown, and 3 for olive; ventral color: 1 for white, 2 for yellowish, 3 for yellow, and 4 for intense yellow; underpart markings: 1 for few, 2 for intermediate amount, and 3 for densely marked.

shape component (PC2) with longitude, but not with latitude. Such relationships were lacking for females. The large percentage of variance (64.6%) explained for male measurements by PC1 and the positive loadings of all the morphological variables (Table 3) clearly indicate that the PC1 axis is a size or feather length vector. Furthermore, 96.5% (50.0% + 46.5%; Table 3) of the total variance from the first principal component is represented by the tail and wing measurements, body size indicators in birds (James 1970, Brumfield and Remsen 1996). The first principal component demonstrates a significant latitudinal and longitudinal trend where northwestern male specimens were the largest, mid-continental ones the smallest, and eastern coastal specimens intermediate (Fig. 3A). The second principal component, the shape component, was related to a bipolar (inverse) relationship between wing and tail that explained 92.3% (44.6% + 47.7%) of total variance for males from that second principal axis (Table 3). As shown in Fig. 3B, PC2 was correlated with longitude ($r = 0.247$, 327 df, $P < 0.005$; Table 2) where western specimens had proportionally longer tails and shorter wings when compared to eastern specimens.

The results of the multivariate analysis of color demonstrate geographic trends more clearly than body size (Table 2). When comparing both sexes, we observed similar patterns in dorsal and ventral coloration (Table 4). The geographic trend (Fig. 4A, B) was that western specimens were lighter ventrally and more gray dorsally than the most eastern birds, which were more yellow ventrally and more olivaceous dorsally. In addition, the amount of underpart markings in females decreased from east to west while the ventral and dorsal color patterns became more saturated. The underpart markings of males displayed no clear geographic pattern, with only

TABLE 2. Coefficient of correlation (*r*) and *P* values from regression of principal component analysis and multiple correspondence analysis characters scores of Northern Waterthrushes against longitude and latitude.

	Latitude				Longitude			
	Males[a]		Females[a]		Males[a]		Females[a]	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
PC1	0.220	<0.001	0.029	>0.05	0.174	<0.002	0.077	>0.05
PC2	0.095	>0.05	0.029	>0.05	0.247	<0.001	0.027	>0.05
MC1	0.251	<0.001	0.384	<0.001	0.280	<0.001	0.482	<0.001

[a] df = 327 for males, 159 for females.

TABLE 3. Principal component analysis character scores from morphometric variables in male and female Northern Waterthrushes.

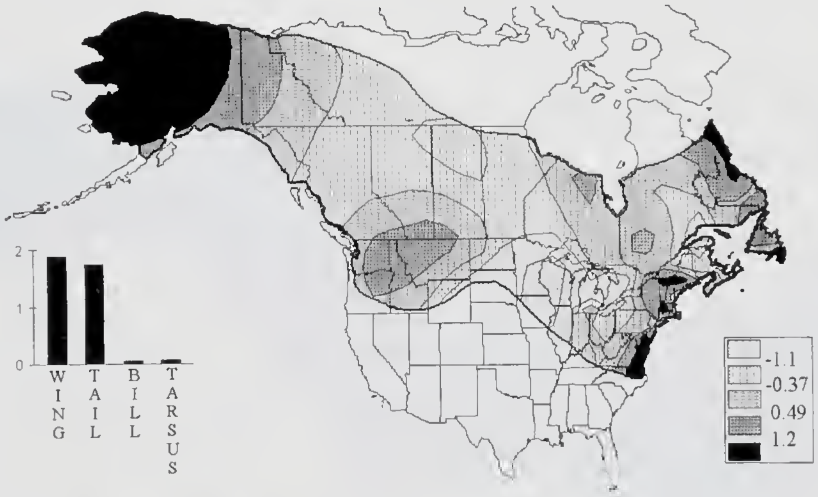
	PC1				PC2			
	Males		Females		Males		Females	
	Scores	Row inertia[a]	Scores	Row inertia[a]	Scores	Row inertia[a]	Scores	Row inertia[a]
Wing cord	1.879	50.0	2.128	49.2	−1.127	−44.6	−1.239	−46.1
Tail length	1.747	46.5	2.026	46.9	1.205	47.7	1.295	48.2
Bill length	0.059	1.6	0.088	2.0	0.084	3.3	0.090	3.4
Tarsus length	0.073	1.9	0.080	1.9	0.110	4.3	0.061	2.3
Variance explained (%)		64.6		69.1		26.9		25.8

[a] The row inertia gives the percentage of each individual variable contributing to the total variance of a principal axis.

8.9% of the variance from that variable explained by the first axis (Table 4).

Size tendencies and described subspecies.—Differences in male wing length (means ± 95% confidence intervals) allowed the separation of *S. n. uliginosus* from *S. n. notabilis* and *S. n. limnaeus* ($F = 6.47$, 3 df, $P = 0.004$. *Seiurus n. uliginosus* had the longest wing (76.8 ± 0.6) compared to *S. n. notabilis* (75.6 ± 0.3) and *S. n. limnaeus* (74.0

A) PC1: ♂ morphometric characters



B) PC2: ♂ morphometric characters

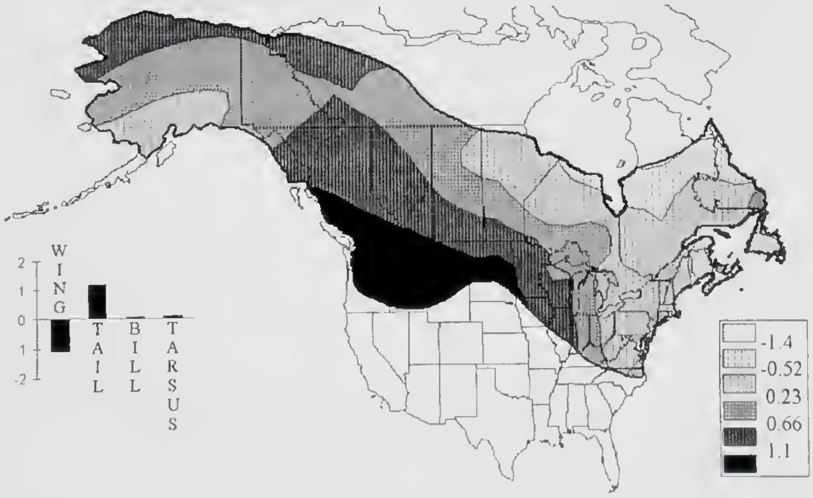


FIG. 3. Isocontours from principal component analysis (PC1 for size and PC2 for shape) of male morphometric characters in Northern Waterthrushes. Histograms represent the relative contribution of each individual variable to the total variance of a principal axis (see Table 3). The legends on the right indicate the limit values between isocontour shades.

TABLE 4. Multiple correspondence analysis of character scores from the first axis of color measurements in male and female Northern Waterthrushes.

	Males		Females	
Color classes[a]	Scores	Correlation ratio[b]	Scores	Correlation ratio[b]
Dorsal coloration		66.3		41.8
Dark brown (1)	0.756		0.453	
Olivaceous brown (2)	0.343		0.713	
Olive (3)	−1.340		−0.623	
Ventral coloration		60.5		59.9
White (1)	1.871		−0.491[c]	
Yellowish (2)	0.571		0.738	
Yellow (3)	−0.384		−0.838	
Intense yellow (4)	−3.082		−0.706	
Underpart markings		8.9		41.7
Few markings (1)	−0.240		−1.889	
Intermediate (2)	0.187		0.039	
Densely marked (3)	−0.582		0.777	
Percentage of variance explained		19.4		20.5

[a] In parentheses: numerical values given to each color class.

[b] The correlation ratio indicates the percentage of variance coming from the modalities of a variable explaining a multiple component axis.

[c] This value was omitted from the discussion because of its small sample size; 4 specimens out of 161 females represent the modality number one in the ventral color.

± 1.0). The same was true for females ($F = 5.00$, 3 df, $P = 0.026$), *S. n. uliginosus* had a longer wing (74.7 ± 0.9) than *S. n. notabilis* (73.3 ± 0.5) and *S. n. limnaeus* (71.3 ± 0.8). The difference in female wing length between *S. n. uliginosus* and *S. n. noveboracensis* (73.1 ± 0.8) was not significant.

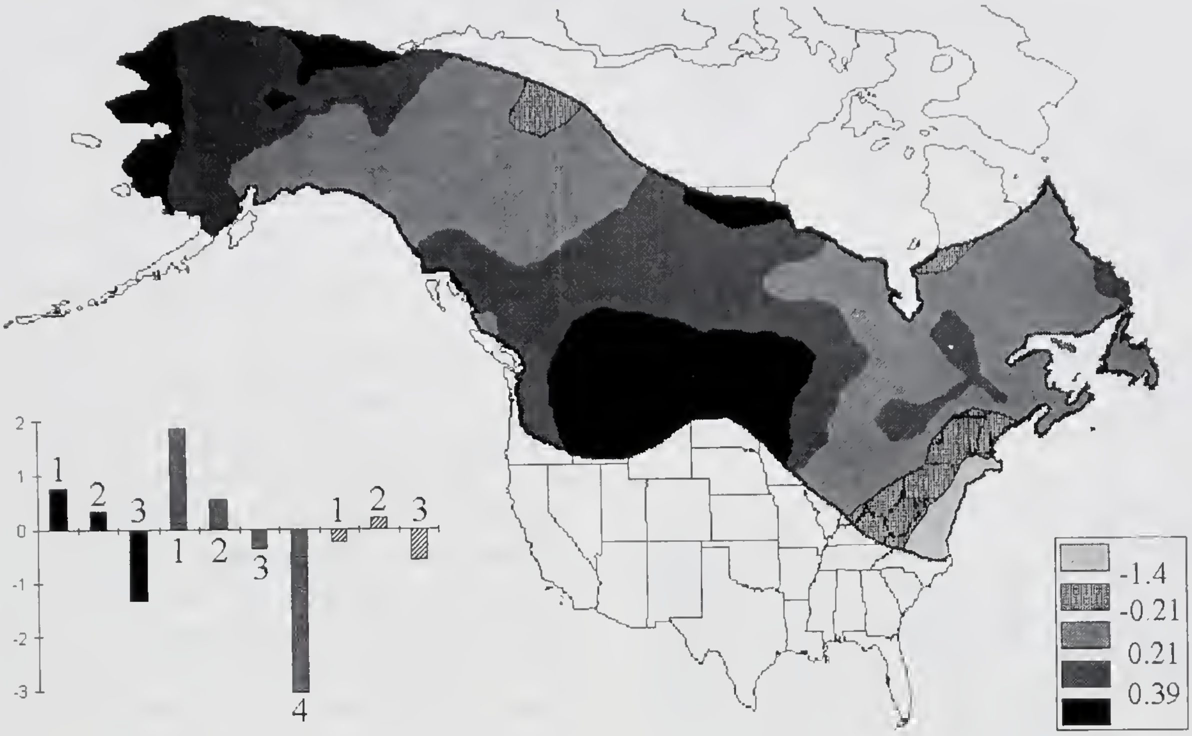
In males, tarsus length allowed the discrimination of *S. n. notabilis* from both *S. n. noveboracensis* and *S. n. uliginosus* ($F = 6.30$, 3 df, $P < 0.001$). In this case, the tarsus was smaller in the easternmost subspecies, *S. n. noveboracensis* (20.35 ± 0.18) and *S. n. uliginosus* (20.26 ± 0.25) than in *S. n. notabilis* (20.66 ± 0.10). The difference in bill length between *S. n. notabilis* and *S. n. uliginosus* was not significant, although nearly so ($F = 2.52$, 3 df, $P = 0.0571$). *S. n. notabilis* had a longer tail than *S. n. noveboracensis* ($F = 3.35$, 3 df, $P = 0.0193$).

Color tendencies and subspecies.—In both sexes, *S. n. notabilis* differed from *S. n. uliginosus* by its dorsal (males: $F = 13.75$, 3 df, $P < 0.001$; females: $F = 11.5$, 3 df, $P < 0.001$) and ventral coloration (males: $F = 29.42$, 3 df, $P < 0.001$; females: $F = 23.70$, 3 df, $P < 0.001$). It also varied from *S. n. noveboracensis* by the dorsal coloration in males ($F = 13.75$, 3 df, $P < 0.001$) and the ventral coloration in both sexes (males: $F = 29.42$, 3 df, $P < 0.001$; females: $F = 23.70$, 3 df, $P < 0.001$). Finally, *S. n. uliginosus* differed from *S. n. limnaeus* by the ventral coloration in males ($F = 29.42$, 3 df, $P < 0.001$) and by the dorsal coloration in both sexes (males: $F = 13.75$, 3 df, $P < 0.001$; females: $F = 11.5$, 3 df, $P < 0.001$). The eastern populations, *S. n. uliginosus* and *S. n. noveboracensis,* were generally more olive dorsally and more yellow ventrally than the western populations. Ventrally, 82% (74% + 8%) of *S. n. uliginosus* and 74% of *S. n. noveboracensis* were from the yellowest categories whereas only 28% of *S. n. notabilis* and 39% of *S. n. limnaeus* were from the same categories (Table 5). Dorsally the differences were smaller but 29% of *S. n. uliginosus* and 44% of *S. n. noveboracensis* were from the most olive category whereas only 23% of *S. n. notabilis* and 6% of *S. n. limnaeus* of the westernmost populations were from the same category.

DISCUSSION

Our data clearly indicate that adult males are larger than adult females and that size dimorphism, very strong in the wing, tail, and bill, is greater than previously reported (Ridgway 1902, Eaton 1957, Godfrey 1986, Eaton 1995). The greater size dimorphism could be explained by the exclusion of juveniles from

A) ♂ color characters



B) ♀ color characters

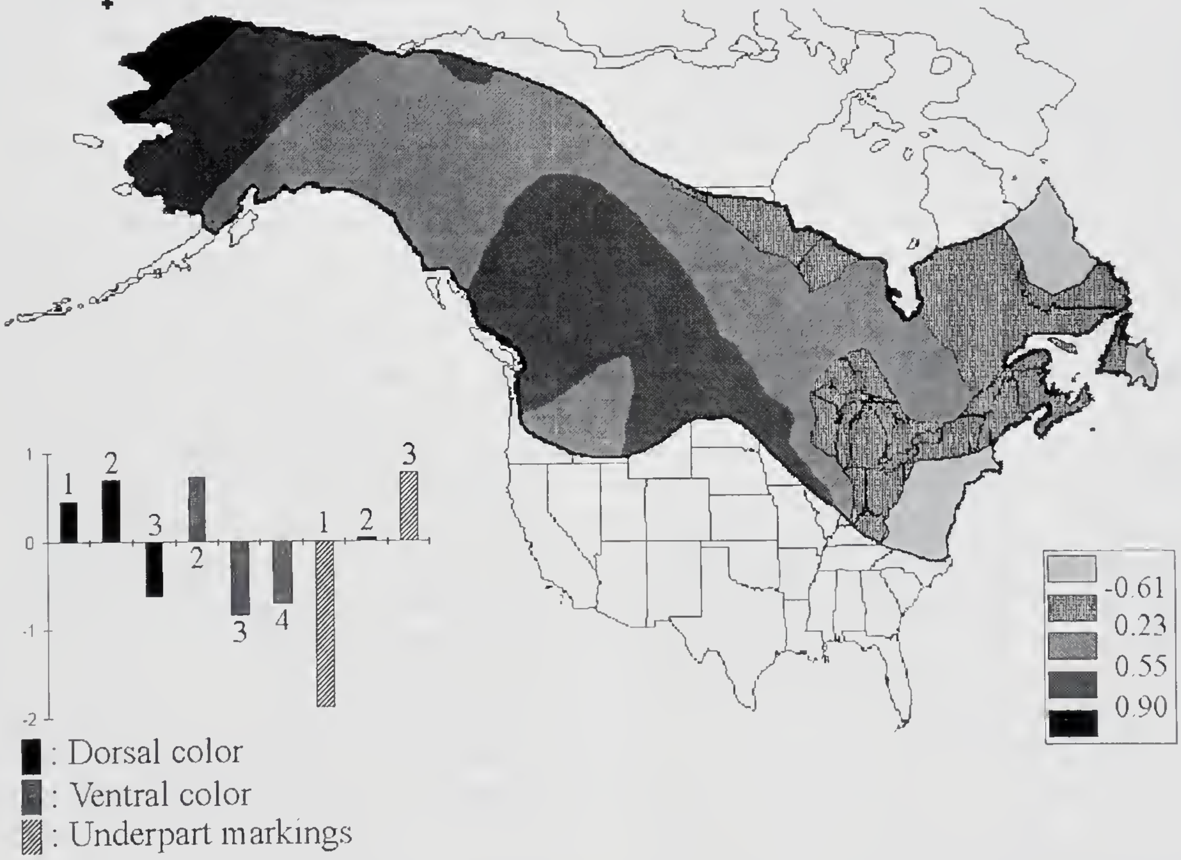


FIG. 4. Isocontours from multiple correspondence analysis (MC1) of male (A) and female (B) Northern Waterthrushes. Histograms represent the relative contribution of each color class category to the total variance of a principal axis. Dorsal color: 1 = dark brown, 2 = olivaceous brown, 3 = olive; ventral color: 1 = white, 2 = yellowish, 3 = yellow, 4 = intense yellow; underpart markings: 1 = few, 2 = intermediate amount, 3 = densely marked. The legends on the right indicate the limit values between isocontour shades.

TABLE 5. Percentage of specimens from each color class clustered by subspecies.

Subspecies	Dorsal coloration			Ventral coloration			
	Dark brown	Olivaceous brown	Olive	White	Yellowish	Yellow	Intense yellow
S. n. uliginosus	0%	71%	29%	0%	18%	74%	8%
S. n. noveboracensis	11%	45%	44%	0%	26%	65%	9%
S. n. notabilis	28%	49%	23%	3%	69%	27%	1%
S. n. limnaeus	22%	72%	6%	0%	61%	39%	0%

our data, an accurate identification of sexes in the process of preparing the specimens, and the use of specimens captured only during the breeding season.

Only males showed geographic variation in size (Table 1). When describing the subspecies of *Seiurus noveboracensis,* Ridgway (1902), McCabe and Miller (1933), and Burleigh and Peters (1948) discussed both sexes, but in reality, their samples contained mainly males because females were not available in any significant number in collections at the time (25 females were used by McCabe and Miller and 8 females were used by Burleigh and Peters). In our case, the absence of significant morphometric geographic variation in females (Table 1), in spite of our large sample size (161 females), is surprising.

In agreement with James' (1970) observations on the patterns of geographic size variation in birds in the eastern and central United States, size in males gradually increased northward, which is consistent with "Bergmann's Rule", and westward. There was no clear geographic grouping of specimens based on size but instead, a complex cline. This cline illustrates that the most northwesterly specimens were the largest and that wing and tail lengths decreased gradually eastward (Figs. 2A, B, 3A) with the smaller individuals in the center of the continent. We also noted another increase in size from the Great Lakes towards the east coast.

The trend in bill size is the opposite. Eaton (1957) related the trend to Allen's Rule, which states that animals living in warmer climates have longer extremities. Earlier, Ridgway (1902) reported that bills in the southwestern portion of the range were longer than those from eastern populations. However, McCabe and Miller (1933) found that bills from the southwestern populations were shorter.

Body shape (Fig. 3B) exhibits a more consistent clinal variation than size (Fig. 3A). The shape principal component is a tail/wing relationship. Western specimens tend to have proportionally longer tails than wings when compared with specimens coming from the eastern part of the range. The tail/wing ratio is lowest on Newfoundland, in southeastern Quebec, and in New Brunswick. This may explain why Ridgway (1902) and Burleigh and Peters (1948) observed so much difference between western and eastern birds. The absence of sudden breaks in shape variation (Fig. 3B) indicates that this trend, as well as size variation, is clinal. Such trends appear to be associated with environmental components such as climate (James 1970, Aldrich and James 1991, Bronner 1996).

Our findings are consistent with Eaton's (1957) with regard to dorsal and ventral color variation. Specimens from eastern states (West Virginia, Ohio, Pennsylvania, Maryland, Delaware, New Jersey, New York, Connecticut, Rhode Island, Massachusetts, New Hampshire, Vermont, and Maine) are more yellow ventrally and more olivaceous dorsally. The strong association between the two characters suggests that a "yellow coloration" is involved here. In females, the increase in yellow is accompanied by a significant decrease of the markings on the breast (Table 4). The apparent cluster of specimens having more yellow does not correspond to any subspecies distribution. It is tempting to attribute yellow color to *S. n. uliginosus* because this form represents the typical easternmost birds.

Du Mont (1930) stressed the difficulty in distinguishing between *S. n. noveboracensis* and *S. n. notabilis* in the Mississippi Valley. Cory (1909) proposed the Mississippi Valley as the border between *S. n. noveboracensis* and *S. n. notabilis.* This region seems to coincide with an intermediate zone of wing length for males (Fig. 2A), size variation contained in PC1 (Fig. 3A), and color patterns (Fig. 4A, B) in both sexes. However, this region is not a border but a section of a complex cline (Figs. 2A, 3A). Furthermore, because the differences between the groups are slight and difficult to interpret, McCabe and Miller (1933:196) concluded "either three subspecific names or none should be employed to suggest conditions known to exist". Taverner (1938) found the distinctions between *S. n. noveboracensis* and *S. n. notabilis* were so fine that they could be disregarded.

Our study does not support the existence of morphologically distinct populations in the Northern Waterthrush. Although *S. n. uliginosus* and *S. n. limnaeus* can be differentiated on the basis of wing measurements alone, the geographic variation in the other size variables shows too much overlap to confirm the validity of the previously described subspecies. There is an interesting variation in body shape (Fig. 3B), but it is mainly clinal; the western specimens have proportionally longer tails and shorter wings than eastern ones. A similar cline is also observed in color variations. However, when describing the size and color differences between the four subspecies, we assumed that the ranges between the subspecies (Fig. 1) did not overlap. This assumption enabled us to analyze the validity of the four subspecies based on our new data set of morphological and color variables. If strong differences between the subspecies had been found (which is not the case), one could argue that those differences would have been less likely if the range overlaps were appreciable.

The particular pattern of variation in size and coloration may also be attributed to the degree of genetic differentiation within this species. When compared to other members of the same family, Barrowclough and Corbin (1978) noticed that the Northern Waterthrush was genetically more heterogeneous than 14 other parulid species. A more detailed genetic analysis of populations and a study of winter distribution patterns compared to breeding distribution could help in further evaluating the validity of subspecies in the Northern Waterthrush.

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MOVEMENT AND TERRITORIALITY OF WINTERING HERMIT THRUSHES IN SOUTHEASTERN LOUISIANA

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ABSTRACT.—We describe the spatial organization and social behavior of Hermit Thrushes (*Catharus guttatus*) wintering in pine plantations and an adjacent hardwood forest in Tangipahoa Parish, Louisiana over three winters. We used point counts (n = 403) to collect data on agonistic behaviors and relative abundance within the study area. We used mist-netting to study site fidelity on four 9-ha plots within and among years. We used radio-telemetry to measure Hermit Thrushes' movements and territoriality (n = 50). We found that Hermit Thrushes saturated suitable patches within the study area. Most Hermit Thrushes actively defended small [mean = 0.55 ± 0.03 (SE) ha], minimally overlapping (15.90 ± 3.63%) territories throughout the winter. Hermit Thrushes established and maintained territories using the same agonistic behaviors described for breeding birds. A few non-territorial birds (14%) moved among occupied territories, but most were faithful to a larger neighborhood, apparently awaiting a territory vacancy. Territorial behavior and frequency of non-territorial birds did not differ among age and sex classes, suggesting the absence of a sex- or age-based dominance hierarchy. The behavior of Hermit Thrushes conformed to the emerging view that competition for spatially mediated resources on the wintering grounds, such as food or cover, contribute to limiting populations of many species of migrant passerines. *Received 10 Dec. 1999, accepted 11 May 2000.*

The winter behavioral ecology of most species of migratory landbirds is poorly understood. In general, we know that migrant passerines employ a variety of behavioral strategies during the winter to deal with specific environmental conditions (Rappole and Warner 1980, Hagan and Johnston 1992). The species specific behaviors used to deal with spatial limitations have important implications for models of population regulation and the development of conservation strategies (Sherry and Holmes 1996).

Local winter spatial strategies are highly variable among species of migrant songbirds. The absence of breeding activities frees many species to move with the protection of a flock or to live solitary, vagrant lifestyles. Many species, including perhaps a majority of non-flocking migrant passerine species, establish resource-based territories that are defended for at least part of the wintering season (Rappole and Warner 1980, Holmes et al. 1989, Winker et al. 1990). Territory defense and exclusion based only on resource availability are likely indicators that habitat availability and food resources are limiting factors during the winter (Brown 1969). Before questions about habitat and food resource use can be answered, it is necessary to describe the basic winter behavioral ecology of a population or species. Several detailed investigations of territorial wintering migrants have revealed that dominant individuals are able to maintain stable territories throughout the winter, while some subordinate birds are forced into a non-territorial strategy in search of resources (Rappole et al. 1989, Winker et al. 1990, Marra et al. 1993, Wunderle 1995). Floater (non-territorial) behaviors have only recently been recognized within wintering populations (Smith 1978, Winker et al. 1990, Stutchbury 1991), although the behavior may be as common as on the breeding grounds.

Floaters are also considered indicators of habitat and/or food resource limitation, providing important insight into a population's local distribution (Brown 1969). The potentially diverse behavioral patterns of floaters make them difficult to categorize and sometimes difficult to detect.

Among forest thrushes, only Wood Thrushes (*Hylocichla mustelina*) and Bicknell's Thrushes (*Catharus bicknelli*) have been studied on their wintering grounds. Many Wood Thrushes that wintered in Veracruz, Mexico had stable territories, but a large subset of the population exhibited a wandering strategy of spatial use (Rappole et al. 1989, Winker et al. 1990). Similarly Bicknell's Thrushes are territorial on their wintering grounds and some may be floaters (McFarland and Rimmer, pers. comm.). Gram and Faaborg (1997) reported

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that wintering Hermit Thrushes in Mexico also might be territorial.

We investigated patterns of spatial use and social behavior by short-distance migrant Hermit Thrushes (*Catharus guttatus*) wintering in southeastern Louisiana. We hypothesized that intraspecific competition results in a behaviorally mediated system of territoriality. This hypothesis leads to three questions. Does the winter behavior of Hermit Thrushes conform to the standard definitions of territoriality? Do alternative classes of behavior exist within the system of territoriality (i.e., floaters)? Finally, does a dominance hierarchy among sex and age classes affect Hermit Thrushes' spatial distribution?

METHODS

The study area, located in northern Tangipahoa Parish, Louisiana (30° 41′ N, 90 28′ W), is a 30 km^2 loblolly pine (*Pinus taeda*) plantation isolated by a mixed landscape of riverine hardwood forest, agricultural land, and rural housing. The pine plantation is a mosaic of even-aged stands ranging in size from 2 to 244 ha [mean = 53.84 ± 9.59 (SE) ha] and represents a continuum of age classes from clearcut to mature forests (20–30 years).

We conducted point counts for three winters (1996–1997, 1997–1998, 1998–1999) during five distinct periods: arrival (15–31 October), fall (1–30 November), early winter (1 December–31 January), late winter (1 February–14 March), and spring (15 March–30 April). We located all point counts within the study area but outside of mist-netted plots. Point count locations were seperated by at least 120 m. Three observers conducted 422 point counts at 191 locations.

We used point counts (n = 120) conducted during the arrival and fall periods to study arrival time, relative abundance, and intensity of vocalizations in the study area. Arrival and fall point counts were conducted as 10 min silent surveys without any playback solicitation. We repeated 40 replicate point counts twice during the arrival period and once during the fall period at ten day intervals.

We used winter and spring point counts (n = 283) to quantify relative abundance and agonistic behaviors. Winter and spring point counts always began with a 10 min quiet period, followed by 5 min of playback recordings of Hermit Thrush songs and calls. For all point counts, we counted Hermit Thrushes and recorded the time, distance, and method by which each Hermit Thrush was originally detected, and the occurrence of agonistic displays. We tested for changes in the level of vocalizations through fall and winter using contingency table analysis of detections with and without playback.

We used four 9-ha study plots, each with 28 mistnets arranged in a grid, to study the movements, site fidelity, and over-winter persistence of individual birds. We passively netted each plot for 2 days (one period) every 5–6 weeks from November to April for all three winters. In addition, once each year in early winter and again in late winter we used playback recordings and a decoy in an attempt to capture and resight every bird on the plots (Sliwa and Sherry 1992, Graves 1996). All captured birds were color banded and aged as either hatch-year/second-year (HY/SY) or after-hatch year/after-second year (AHY/ASY) based on criteria of Pyle (1997). Dwyer (1998) used a molecular technique to sex many of the Hermit Thrushes captured during the winters of 1996–1997 and 1997–1998. We obtained few behavioral observations of known age (n = 58) and known sex (n = 11) birds because only captured birds could be aged and sexed.

We used radio-telemetry of birds netted on study plots to determine if individuals exhibited territorial or floating patterns of movement, as well as to quantify territory size, rates and distances of movement, and interactions with neighbors. We put radio transmitters on 50 Hermit Thrushes captured on the four study plots with transmitters weighing 1.8 grams (Wildlife Materials Inc.), attached to a trimmed interscapular feather tract with epoxy glue.

A single observer triangulated bird locations, usually with at least three bearings, and separated consecutive locations by at least 45 min to insure independence (Swihart and Slade 1985, White and Garrot 1990). We estimated locations to be accurate to within 5 m at a distance of 100 m based on triangulation to transmitters at known locations. We plotted locations by hand, and used RANGES V for spatial analysis of territory size, distance moved between locations, and interaction between neighboring individuals (Kenward and Hodder 1996). We estimated territory size with the minimum convex polygon (MCP) method after visual comparisons with more robust harmonic mean and Kernel methods showed that MCPs estimated biologically meaningful home ranges with fewer location samples. We used incremental analysis, which plots changes in territory size as sample size increases, to determine the minimum number of locations necessary for a good MCP estimate of territory size. We identified floaters by visual inspection of the distribution of MCP size among individuals. We measured movement rate of individuals as the straight-line distance between consecutive locations.

Amount of territory overlap provides information on level of saturation and potential for interaction between neighbors. Measuring territory overlap requires simultaneously radio-tracked groups of individuals and biologically meaningful estimates of territory boundaries. We used harmonic mean estimates of territory boundaries to compute overlap because they visually reflected the areas used most intensely by radio-tagged birds better than MCP or Kernel methods. Harmonic mean home range estimates are extremely biased to grid cell spacing (White and Garrot 1990). We used the program TRACKER (Angerbjorn 1994) instead of RANGES V for this analysis because it suggests a grid cell spacing based on the density of locations. Because harmonic mean estimates of home range are more robust when built from large sample sizes, we limited the analysis of territory overlap to birds with at least 30 locations.

Dynamic interaction is a measure of the attraction, repulsion, or indifference between neighboring individuals. It uses temporally coinciding locations to compute the distance between actual locations of an individual and randomly selected potential locations of its neighbor. Because there was some overlap in the neighborhood of nine simultaneously tracked birds, we conducted a dynamic interaction analysis to determine if pairs of birds were actively avoiding each other. Dynamic interaction analysis is based on Jacob's Index; calculated with Ranges V; Kenward and Hodder 1996). Jacob's values approaching 1.0 indicate that simultaneous locations of a pair are closer to each other than the distance between their territory centers given equal likelihood that they could be anywhere on their territory at that time. Values approaching −1.0 indicate birds are farther away from each other than by chance alone. We used SYSTAT 8.0 for all non-spatial statistical analysis, statistics are reported as mean ± SE.

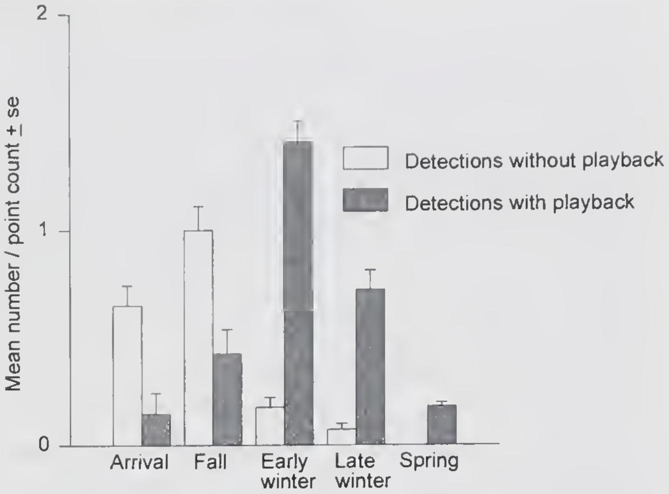

FIG. 1. Point count detections of Hermit Thrushes in southeastern Louisiana with and without playback of Hermit Thrush vocalizations. Detections without playback are dependent on vocalizations by Hermit Thrushes, while total detections with and without playback more accurately reflect actual density. Arrival = 15–31 Oct., fall = 1–30 Nov., early winter = 1 Dec.–31 Jan., late winter = 1 Feb.–14 Mar., spring = 15 Mar.–30 Apr.

RESULTS

Fall point count surveys showed that Hermit Thrushes began to arrive on their wintering grounds in southeastern Louisiana during the second week of October. Density and abundance increased rapidly and stabilized by the end of the third week in October. Territorial vocalizations as measured by point count detections without playback increased with population density and peaked in the fall before declining early in winter (Fig. 1). Density, as measured by number of detections with playback, remained high through the early winter period, although the frequency of vocalizations declined as indicated by fewer birds detected during the silent period of point counts ($\chi^2 = 109.83$, $n = 260$, $P < 0.001$).

We detected 263 Hermit Thrushes at 283 winter points counts with at least one detection at 52% of locations. Only 11% of the Hermit Thrushes we detected at winter point counts were detected before the playback of vocalizations.

Wintering Hermit Thrushes displayed a variety of agonistic behaviors, most of which are commonly used on the breeding grounds (Dilger 1956, Jones and Donavon 1996). At winter point counts with playback, 82% of Hermit Thrushes were first detected by *chup* notes. Only 2% were first detected visually. Almost all non-playback detections were by *chup* notes. Other detections were made by a high pitched *wheez* note (10%), a catbird-like *rank* vocalization (3%), and wing winnows (1%; see description of behaviors in Jones and Donovan 1996). We heard singing in the form of soft, whispering song several times both with and without playback, usually soon after fall migration. Common agonistic visual displays included tail- and wing-flicking, crest raising, foot quivering, bill snapping, puffing, and stretching. We recorded agonistic displays during almost every visual observation that followed playback recording of Hermit Thrush vocalizations.

Intraspecific agonistic interactions between two or more Hermit Thrushes, such as chasing or perch displacement, were observed in about 21% of playback events. We recorded behaviors of 11 individuals of known sex and 58 individuals of known age. Females ($n = 9$) and males ($n = 2$) displayed most of the common aggressive behaviors. Similarly, all behaviors were observed in both HY/SY ($n = 43$) and AHY/ASY ($n = 15$) age groups.

We captured 206 individual (newly banded) Hermit Thrushes in 24,416 hours of passive mist-netting. Thirty-seven percent of all captured individuals were AHY/ASY and 74% of 82 sexed individuals were female (Dwyer 1998). Capture rate of Hermit Thrushes including recaptures (within the same year), returns (between years), repeats (same day or period), and unbanded birds was 1.4 per 100 net-h. We captured 65 additional individuals and 24 recaptures using playback and decoys, for a total of 271 individuals captured. We recaptured 95 (35%) of these within a year (but different period). Twenty-five (18% of individuals banded in the first and second years) returned in subsequent years to winter on the same study plot. The age ratio of returning individuals in their first year of capture did not differ from the age ratio of all individuals captured ($\chi^2 = 0.21$, $n = 323$, $P > 0.05$). Similarly, the sex ratio of returning Hermit Thrushes (75% of 12 were female) did not differ from the overall ratio in the study area (Fisher Exact Test: $\chi^2 = 0.03$, $n = 94$, $P > 0.05$). Of the 25 returns only two were captured more than 30 m from the net where they were originally captured. We never captured or observed any marked Hermit Thrush at more than one 9 ha plot or at more than one point count location.

We radio-tracked 50 Hermit Thrushes. Radios fell off after an average of 21.76 days (±1.98, range = 2–53). During the period when radios were attached, we collected an average of 26.44 (± 2.5, range = 3–63) locations per bird. Incremental analysis of 12 home ranges showed that MCPs begin to plateau after 10–20 locations. Seven radio equipped Hermit Thrushes were categorized as non-territorial based on their large home range sizes. Of the remaining birds, we had enough locations (>10) to make territory size comparisons for 34 Hermit Thrushes. Nine birds with transmitters were not included in the analysis because of small location sample sizes. Territory sizes averaged 0.55 ± 0.03 ha, (range = 0.22–0.97 ha). Territory sizes did not differ between sexes ($F_{1,14} = 0.164$, $P > 0.05$), or between age groups ($F_{1,32} = 1.212$, $P > 0.05$). We located nine birds at night, all roosting within their territories.

Most Hermit Thrushes (85%) maintained territories with a MCP less than 1 ha. We classified seven birds with large MCPs as floaters (5.83 ± 1.06 ha, range = 2.53–11.3; Fig. 2). The average distance between consecutive locations for territorial birds was 55.30 ± 1.59 m. In contrast, floaters moved an average of 121.28 ± 25.36 m between locations, two floaters moved more than 1 km between locations (Fig. 3A). Floaters sometimes displayed aggressive behavior similar to that of territorial birds. One floater was originally captured using playback vocalizations and another responded to playback after its radio failed. Dwyer (1998) sexed two floaters; one was a male and one was female. Age of floaters (5 HY/SY, 2 AHY/ASY) did not differ from the age ratio of all other captured Hermit Thrushes (65% HY/SY).

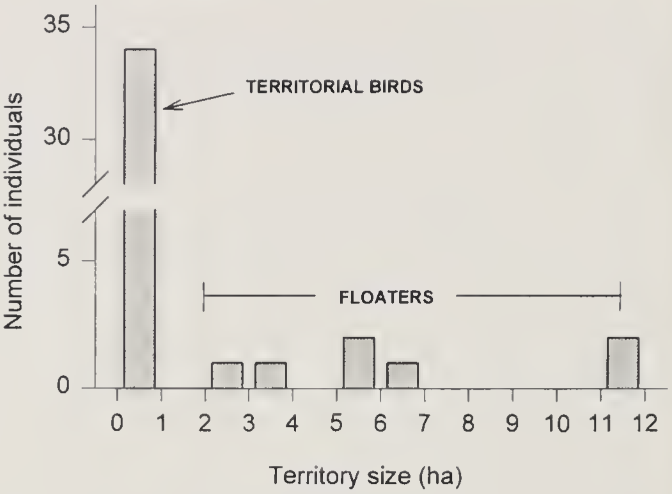

FIG. 2. Minimim convex polygon territory size for 41 Hermit Thrushes. The large gap in the distribution between 34 individuals with territories smaller than 1 ha and 7 individuals with larger territories was used to characterize floaters.

Of nine simultaneously radio-tracked neighboring birds, eight had distinct, abutting territories. The analysis revealed little territory overlap except for one bird that we categorized as a floater. We simultaneously radio-tracked four additional pairs and one triad with overlapping or abutting home ranges. Overlap between territorial birds averaged 15.90% ± 3.63%, $n = 21$) and ranged from 0–79% of territory area (Fig. 3B). Every combination of overlapping pairs scored near zero on Jacob's Index, indicating that birds were indifferent to each other (mean = 0.005 ± 0.005).

DISCUSSION

Banding data indicated that many wintering Hermit Thrushes were site faithful from November to March. Ninety percent of within year recaptures occurred at the same net (45%) or a net within 80 m (the average diameter of a territory). Hermit Thrushes did not move out of their territories to roost elsewhere

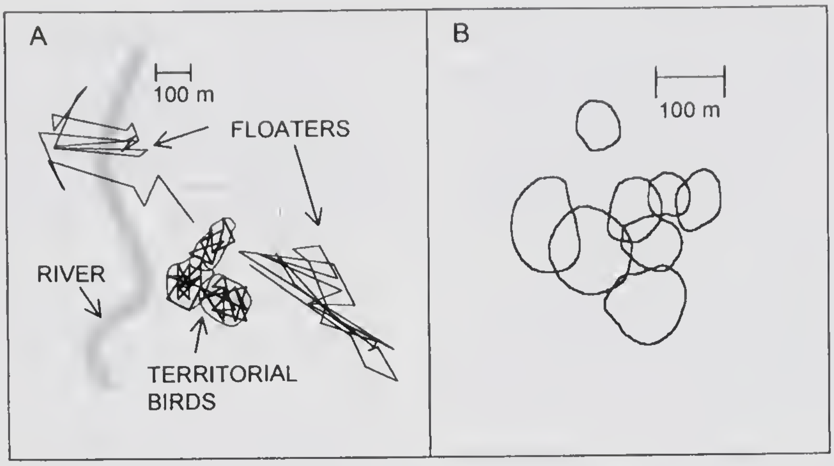

FIG. 3. Movements of Hermit Thrushes wearing radio telemetry transmitters. A. Movement patterns of two floating and three territorial Hermit Thrushes in relation to 9 ha mist-net plot (box). Home range contours are also shown for territorial birds. Lines indicate movements between successive locations. B. Territory contours (95% hamonic mean method) of eight simultaneously radio-tracked Hermit Thrushes showing variation in territory size and overlap among neighbors. A floater that moved among territories of these individuals is not shown.

at night. Although only 18% of Hermit Thrushes returned between winters, the individuals that returned used the same territory as in previous winters. Additional Hermit Thrushes may have returned to the area, but relocated outside of our plots. Telemetry data indicated that most wintering Hermit Thrushes maintained distinct, minimally overlapping territories. High vocalization rates during the initial settlement indicated aggressive territory establishment. The lack of spatial interaction between neighboring individuals and the low level of vocalizations following settlement suggests that once territory boundaries were established, boundary maintenance was minimal.

Hermit Thrushes that did not establish a stable territory in a suitable habitat were lumped into the broad category of floaters. The term floater has been used to describe two different patterns of behavior for non-breeding birds. First, floaters have been characterized as indiscriminate wanderers, perhaps faithful to particular habitats, but not defending specific territories. Usually such floaters are recognized only as individuals not recaptured or resighted in repeated mist-netting and spot-mapping periods (Bates 1992). The second explanation characterizes non-breeding season floaters as secretive but intent subordinates, stalking selected territories in search of vacancies (Smith 1978). In general, floaters are thought to be at a behavioral disadvantage to territorial birds and experience lower survival relative to territory holders (Brown 1969).

Collectively, the floaters we monitored do not fit into either definition but showed a diverse array of spatial strategies. For instance, one radio-tagged bird had a very small core home range but otherwise wandered widely among neighboring territories and surrounding habitats. We suspect this bird may have been looking for a new, less constrained territory but was encountering spatial pressure wherever it wandered. Another individual crossed a 60 m wide river channel more than 10 times during 2 months, moving back and forth between two habitats. Two other Hermit Thrushes moved long distances (0.6 km and 1 km) before radio contact was lost. One pattern was consistent among all the floaters in this study: they chose alternatives to territoriality instead of establishing territories in unsuitable habitats (i.e., clearcuts).

We found no evidence that winter territorial behavior of Hermit Thrushes resulted in dominance of males over females or older over younger age groups, although we had small sample sizes for these comparisons. Females used agonistic calls and displays as did males, and females maintained territories of the same size as males. Males as well as females behaved as floaters, and females returned to the same territory between winters as frequently as males. Similarly, younger Hermit Thrushes used agonistic behaviors to successfully defend territories that did not differ in size from those of older individuals. Finally, younger Hermit Thrushes were no more likely to be floaters and returned between winters at the same frequency as older Hermit Thrushes. Territorial wintering species with obvious morphological differences between age and sex classes, like American Redstarts (*Setophaga ruticilla*) and Hooded Warblers (*Wilsonia citrina*), quickly sort into distinct dominance hierarchies after arriving on their wintering grounds (Holmes et al. 1989, Stutchbury 1994). In contrast, the subtle morphological differences between age and sex classes of Hermit Thrushes may be related to our failure to detect a dominance hierarchy. The absence of dominance hierarchies during the winter might be expected in other monomorphic migrant species (Bates 1992).

We have provided four types of evidence that suggest Hermit Thrushes saturate suitable patches within the local landscape. First, Hermit Thrushes aggressively defended resources with agonistic vocalizations and displays that are also used on breeding grounds for territory defense. Second, Hermit Thrushes occupied distinct home ranges that abut or slightly overlap with neighboring conspecifics. Third, some individuals behaved as floaters, moving within and among territories of other individuals. Finally, vacated territories were quickly occupied by either expanding or shifting neighbors, or floaters. Two territories vacated by Sharp-shinned Hawk (*Accipiter striatus*) predation were reoccupied within one week by vocalizing Hermit Thrushes. We do not know if replacements were floaters or territorial neighbors that occupied the open space. In either case, rapid replacements indicate saturation.

Wintering Hermit Thrushes defended smaller territories at higher densities than eastern populations of breeding Hermit Thrushes. Martin (1960) estimated territories in Ontario, Canada averaged 0.72 ha. Jones and Donovan (1996) reported mean sizes of 2.5 ha (range = 0.5–14.3) from 12 breeding season studies. In comparison, we estimate 0.56 ha based on telemetry data from all plots. Our estimates of territory size are similar to those found for Wood Thrushes wintering in Veracruz, Mexico (Winker et al. 1990).

Winker and coworkers (1990) using telemetry, estimated that 50% of the Wood Thrushes in Veracruz, Mexico were floaters, compared to 14% of Hermit Thrushes in our study. The higher proportion in Mexico might be caused by more pronounced habitat limitations than occur in southeastern Louisiana.

Site fidelity between winters is an important indicator of breeding season survivorship and winter habitat quality. The proportion of Hermit Thrushes returning between winters in our study is lower than for all other studied species of migratory passerines. Other researchers on wintering passerines report overwinter returns near 50% (Nisbet and Medway 1972, Price 1981, Winker et al. 1990). Differences may be due to species-specific survivorship and dispersal patterns. Other studies of wintering Hermit Thrushes report return rates similar to ours. In South Carolina, 13% of 81 birds returned between winters (Bent 1964), and in California, 18% of 306 returned between winters (reported in Jones and Donovan 1996). Estimates for Hermit Thrushes, including our own, might be biased low by sampling methods or species-specific behaviors. Long-term studies would allow for more robust mark-recapture analyses and increase the accuracy of these estimates.

The behaviors of wintering Hermit Thrushes in southeastern Louisiana clearly conform to Nice's definition of Type-E winter territories (Nice 1941). Territoriality in non-breeding migrants is now a widely recognized behavior, but its function in population regulation is not fully understood (Rappole and Warner 1980). The evidence for overlapping territories and the presence of a floater class confirms that the distribution of wintering Hermit Thrushes in southeastern Louisiana agrees with Brown's (1969) Critical Density Level 3. Most birds actively defend distinct, minimally overlapping territories, probably in response to some limiting resource (i.e., food or space).

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EFFECT OF PREDATION AND COWBIRD PARASITISM ON THE NESTING SUCCESS OF TWO SYMPATRIC NEOTROPICAL MARSHBIRDS

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ABSTRACT.—We compared the effect of nest predation and cowbird parasitism on the breeding success of two simultaneously nesting ecologically similar blackbird species that differ in their breeding strategies. The Scarlet-headed Blackbird (*Amblyramphus holosericeus*) is a monogamous species that performs territorial defense. In contrast, the Brown-and-yellow Marshbird (*Pseudoleistes virescens*) is a non-territorial monogamous breeder that performs mate guarding and has helpers at the nest. Both species suffered similar nest predation rates throughout their nesting cycle. However, the Brown-and-yellow Marshbird suffered higher parasitism from Shiny (*Molothrus bonariensis*) and Screaming cowbirds (*M. rufoaxillaris*) than the Scarlet-headed Blackbird (62.6% vs 15.4%). Brood parasitism accounted for most of the egg losses and hatching failures in Brown-and-yellow Marshbird. Parasitized nests had lower egg survival and hatching success than non-parasitized ones. Mean clutch size was 1.5 eggs larger in Brown-and-yellow Marshbird than in Scarlet-headed Blackbird. However, Scarlet-headed Blackbird had higher hatching success than Brown-and-yellow Marshbird and similar fledging success. Consequently, both species produced similar numbers of fledglings. We did not detect any relationship between the reproductive success of these species and their breeding strategies. The presence of helpers at Brown-and-yellow Marshbird nests did not affect nest defense or chick survival, but helpers might account for reduced parental effort by supplementing food delivery to chicks/fledglings. *Received 10 Nov. 1999, accepted 15 May 2000.*

Avian reproductive strategies can result from the influences of ecological factors including the temporal and spatial patterns of food distribution, the form and intensity of predation on both adults and nests (Lack 1968, Ricklefs 1969, Emlen and Oring 1977, Picman 1988), and their evolutionary history (Brooks and McLennan 1991). Typically, studies of comparative nesting success focused on how reproductive traits such as clutch size, brood size, and nestling stage length may be affected by selective forces such as food availability, territory quality, and predation risk (e.g., Lack 1968; Ricklefs 1969; Slagsvold 1982; Martin 1987, 1992, 1995). Less frequently, nesting performance and reproductive traits have been related to mating systems and reproductive behavior (but see Post 1986, Larsen et al. 1996).

Chick and egg predation have been suggested to be the main causes of nesting failure in terrestrial birds (Ricklefs 1969, Picman 1988, Martin 1995). Nest predation reduces parental fitness and might be expected to select for parental breeding traits and strategies to reduce the predation risk (Meilvang et al. 1997). Accordingly, several researchers have recognized predation as a major factor affecting such diverse aspects of breeding strategies as the spacing pattern of nesting (Lack 1968, Post 1986, Martin 1988) and parent investment on nesting attempts (Skutch 1949, 1985; Martin 1992).

Different benefits and costs have been proposed relating to the spacing pattern of nests. Nesting in a territorial pattern with a high intra- and interspecific defense of the territory has been suggested to reduce brood parasitism (Robertson and Norman 1977) and losses from predators by reducing conspicuousness (Lack 1968). On the other hand, clumping of nests could be advantageous because it increases the detection of predators from a greater distance (Burger 1974), clumping nests also makes possible defense by cooperative mobbing (Wiklund and Anderson 1980) or by dilution effect (Robertson 1973).

Intraspecific comparisons have shown that traits such as timing of breeding or even

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TABLE 1. Comparison of breeding strategies of Brown-and-yellow Marshbirds and Scarlet-headed Blackbirds. Sources: Orians et al. 1977; Orians 1980; Mermoz and Reboreda 1998.

Behavior	Brown-and-yellow Marshbird	Scarlet-headed Blackbird
Mating system	monogamous	monogamous
Nesting habitat	marshes, edges of marshes and humid grasslands	marshes
Mate guard after nest is built	yes	no
Territorial defense	no	yes
Presence of helpers at the nest	yes (usually at nestling stage)	no
Chick feeding	both parents and helpers	both parents

clutch size could vary with environmental conditions (Murphy 1983, Brawn 1991). Studies of species that breed simultaneously could control for variance because these species experience the same general predator assemblage and the same macroclimate conditions (Martin and Ghalambor 1999). Thus, contemporaneous studies of sympatric, closely related and ecologically similar species are particularly useful for characterizing reproductive patterns and identifiying an ecological basis for life history differences (Murphy 1988, Ramstack et al. 1998).

In this work we compare the nesting success and reproductive traits of two sympatric, closely related Neotropical marshbirds breeding in the same area during 1995–1997; the Scarlet-headed Blackbird (*Amblyramphus holosericeus*) and the Brown-and-yellow Marshbird (*Pseudoleistes virescens*). Both species are monogamous open cup-nesters and have similar morphological and ecological characters, but differ in their reproductive strategies. The Scarlet-headed Blackbird performs an active territorial defense; the Brown-and-yellow Marshbird is a non-territorial breeder that performs mate guarding and has helpers at the nest (Orians 1980). The cooperatively breeding Brown-and-yellow Marshbird may experience higher predation rates than the non-cooperatively breeding Scarlet-headed Blackbird (Orians et al. 1977, Orians 1980). Although helpers collaborate in nest defense, predation affects more than 80% of Brown-and-yellow Marshbird nests (Mermoz and Reboreda 1998).

Our objective was to determine whether differences in life histories and breeding strategies between these species account for differences in their nesting success. Territorial defense performed by Scarlet-headed Blackbirds might reduce nest predation risk and cowbird parasitism; however, it could reduce the food delivery to nestlings once they hatched. Brown-and-yellow Marshbird mate guarding behavior could increase the time that a nest remains unattended exposing it to greater nest predation. Helpers at the nest in this species could increase the amount of food delivery to nestling.

METHODS

Study species.—The Scarlet-headed Blackbird inhabits marshes of southern Brazil, Paraguay, Uruguay, and eastern and northeastern Argentina (Ridgely and Tudor 1989). They are gregarious during the non-reproductive season (Sclater and Hudson 1898, Gibson 1918), but they form individual breeding pairs during early spring (August–September). Each nesting pair defends a large territory (up to 50 ha) against all conspecifics and, occasionally, from individuals of other coexisting species (Orians 1980).

The Brown-and-yellow Marshbird inhabits temperate marshy areas and humid grasslands in northeastern Argentina, Uruguay, and neighboring areas of southern Brazil (Ridgely and Tudor 1989). During the nonbreeding season they are highly gregarious and feed in dense groups on the ground (Hudson 1920). During the breeding season they are non-territorial breeders and monogamous. Once chicks hatched, helpers at the nest might deliver food to the chicks (Orians et al. 1977, Orians 1980). Table 1 summarizes the main breeding behaviors of the two species.

Study area.—Nesting data were collected during 1995–1997 breeding seasons (October–December). Nest searching was performed along the sides of an unpaved road (about 15 km long), parallel to an artificial drainage (Canal 2) and along the sides of the route 11 at General Lavalle (36° 20′ S, 56° 54′ W), Buenos Aires Province, Argentina. The habitat is flat and low, characterized by numerous small wetlands and scattered shallow marshes (about 60% of the area), with little of the land rising more than 4 m above sea level. The marshes consisted of mixed patches of bulrush (*Scirpus californicus*), cattails (*Thypha* spp.), *Cyperus* spp., and in some cases broad pure patches of *Solanum malacoxylon.* Water depth was generally 0.3–0.5 m throughout the study period although three marshes were completely dry. On the upland areas, exotic thistles (*Cynara cardunculus, Carduus* sp.) 0.5–1.5 m tall grew along the sides of the road in a continuous row. Flooded areas and marshes surrounded these small upland areas. Native bushes [black-rushes (*Juncus acutus*) and pampa grasses (*Cortaderia selloana*)] were clumped on flooded areas. The study site was surrounded by open fields, used primarily for livestock rearing on natural pastures. Potential nest predators in our study area were Chimango Caracara (*Milvago chimango*), Long-winged Harrier (*Circus buffoni*), opossums (*Lutreolina crassicaudata*), ferrets (*Galictis* spp.), Barn owls (*Tyto alba*), skunks (*Conepatus* spp.), small snakes, and rodents.

We found most of Brown-and-yellow Marshbirds' nests (61.5%) built in thistles in uplands, 23.1% of the nests were built on black rushes in flooding areas (edges of marshes) and 15% were on cattails in marshes. We classified nests as being built on marshes, uplands, or flooding areas (Mermoz and Reboreda 1998).

Nesting biology.—Each nest located was mapped and marked nearby with an inconspicuous coded tag. When the nest was found during incubation, we used the date found, number of eggs, and incubation stage (Hays and LeCroy 1971) to estimate the date of the first egg. Most nests were checked every other day until the young fledged or the nest failed. Each egg was marked with waterproof ink and checked for cracks or punctures. The presence of egg fragments or missing eggs was attributed to partial predation or interspecific brood parasitism by cowbirds (Shiny Cowbird, *Molothrus bonariensis*; Screaming Cowbird, *M. rufoaxilliaris*). Most nests were abandoned after one or several eggs had been removed. To be conservative, we considered those nests that had cowbird eggs or nestlings at any stage to be parasitized. Nests showing either total egg or nestling loss were considered depredated.

Nest survival.—Nest survival was estimated using Mayfield's exposure method, which is based on nest losses over the total number of days nests were under observation (Mayfield 1975, Johnson 1979). The daily nest mortality rate was defined by the number of nests lost or failed divided by the total number of days those nests were under observation (nest losses/nest × day). To calculate nest exposure time we assumed that the length of the interval at which nest loss occurred was one-half of its length (i.e., nest loss occurred in the middle of the interval between our visits; Mayfield 1975). This nest mortality rate was calculated for three nest stages: egg laying, incubation, and nestling. A nest was considered in the egg laying stage when the females were laying eggs. The incubation stage lasted from the day after the laying of the last egg until the hatching of the first (host or parasite) chick. The chick rearing stage lasted from the day the first chick hatched to the day the last nestling of either species fledged. We estimated the variance of this daily nest mortality rate (V) from Johnson's (1979) equation $V = [(\mathrm{ND} - \mathrm{losses}) \times \mathrm{losses}]/\mathrm{ND}^3$, where ND is the number of nest-days of exposure and losses the number of nests that failed. Nest survival at each nesting stage was calculated as $(1 - DNMR)^t$, t being the time of each nesting stage and $DNMR$ the respective daily nest mortality rate. We assumed that daily nest mortality rates remained constant over each stage. Nesting success was defined as the product of the probability of nest survival at each stage (Mayfield 1975). We compared stage-specific nest survival rates using the program CONTRAST (Hines and Sauer 1989).

To control for differences in nest site habitat, interspecific comparisons of nest survival and nesting success were performed considering daily nest mortality rates for each stage of the Scarlet-headed Blackbird and the Brown-and-yellow Marshbird nests built in marshes. We also compared daily nest mortality rates of Brown-and-yellow Marshbirds for nests built in marshes, upland, and flooding areas because this species builds nests in different habitats.

Because brood parasitism was found to have no influence on nest survival (Mermoz and Reboreda 1998), we included all nests we found regardless of parasitism in our analyses. Nests that produced only cowbird fledglings and were not depredated or abandoned were considered successful for this analysis.

Nest attention.—To estimate nest attentiveness during each stage of the nesting cycle, we recorded whether at least one parent was in or near the nest (less than 10 m) on each nest visit during 1996–1997. We made 149 observations at 100 nests of Brown-and-yellow Marshbirds and 140 observations at 36 nests of Scarlet-headed Blackbirds.

Clutch size, egg survival, hatching and fledging success.—Clutch size (total number of eggs laid) was measured from nests found at building or early laying stages. Egg survival was measured as the proportion of the clutch size that remained in the nest until the first egg hatched. Hatching success was estimated as the number of chicks that hatched divided by the total number of eggs present at the end of incubation (Koenig 1982). In some nests, the smallest chick disappeared and we considered this loss as brood reduction (Mock 1994). In 6 Brown-and-yellow Marshbirds' nests and 1 Scarlet-headed Blackbird's nest, we found the smallest chick dead in the nest. In most of those nests, the growth rate of the smallest chick was lower than any of their larger nestmates (Mermoz 1996). Predation was considered as a more probable cause of chick disappearance when the larger ones were missing (Mock 1994). Fledging success was estimated as the number of chicks that fledged divided by the total number of chicks that hatched in successful nests. The effect of cowbird parasitism on egg survival, hatching, and fledging success was evaluated in the Brown-and-yellow Marshbird by comparing these variables in parasitized and non-parasitized nests. The same analysis could not be done in the Scarlet-headed Blackbird because of the small number of parasitized nests.

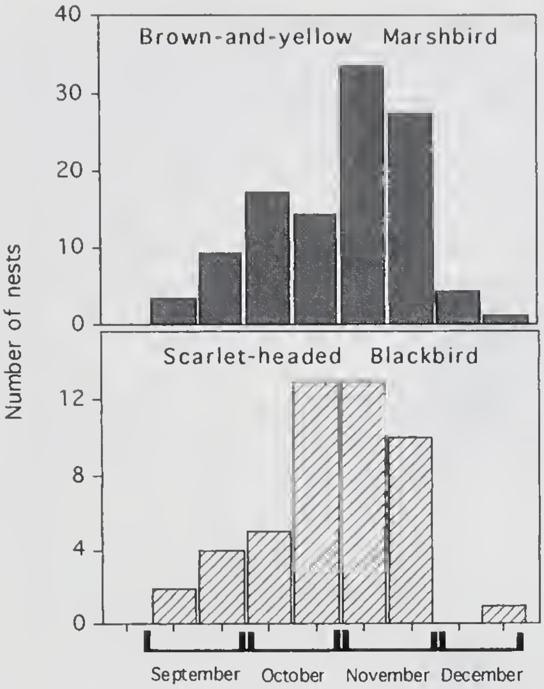

FIG. 1. Total number of nests initiated at different times of the breeding season (15 day interval) of Brown-and-yellow Marshbirds (n = 108) and Scarlet-headed Blackbirds (n = 48).

All measures are presented as mean ± SE of the mean. Statistical analyses were performed using the software StatView 4.51 for Macintosh (1996 Abaccus Concepts Inc.).

RESULTS

General breeding biology.—Scarlet-headed Blackbird pair bonds were first observed 20–30 August, but nests were not found until September (earliest nest found 10–20 September). Similarly, Brown-and-yellow Marshbirds showed breeding activity early in the season and nesting attempts started in September (earliest nest found 1–10 September). For both species, breeding lasted until December (latest nest found 20–30 December).

We found 49 Scarlet-headed Blackbirds' and 129 Brown-and-yellow Marshbirds' nests during the 1995–1997 breeding seasons. The nesting pattern was similar for both species, with the number of nests initiated peaking during November and declining through December (Fig. 1).

Eight of the 49 Scarlet-headed Blackbird nests were renesting attempts and were built on the same territory as the previous failed nest. We observed one instance of two renesting attempts, but most breeding pairs made only one renesting attempt after desertion or depredation. Consequently, 41 Scarlet-headed Blackbird's breeding pairs were followed during this study. The gregarious nesting of the Brown-and-yellow Marshbirds precluded us from assigning renesting attempts because we did not color mark the individuals.

Brown-and-yellow Marshbirds had a larger mean clutch than Scarlet-headed Blackbirds (4.61 ± 0.14 eggs, n = 18, 3.05 ± 0.06 eggs, n = 23, respectively; Mann-Whitney test: $Z = 5.9$, $P < 0.001$). Both species laid eggs at daily intervals and incubation began with the laying of the penultimate egg. The eggs usually hatched after 13–14 full days of incubation and nestlings remained in the nest for about 12 days.

Nest survival.—Twenty-five Scarlet-headed Blackbird's nests (25/41, 60.97%) and 72 Brown-and-yellow Marshbird nests (72/92, 78.26%) were depredated or deserted, in most cases after several eggs were removed from a nest. We excluded the fates of 37 Brown-and-yellow Marshbird and 8 Scarlet-headed Blackbird nests because visit intervals to those nests at the end of nestling stage were more than 5 days (mostly caused by adverse weather). Therefore, we were unable to determine the fate of those nests.

Daily nest mortality rates did not differ with time for the Scarlet-headed Blackbird and the Brown-and-yellow Marshbird ($\chi^2_2 = 3.1$, $P > 0.05$; $\chi^2_2 = 5.46$, $P > 0.05$, respectively). Also, we found no differences between the daily nest mortality rates of Scarlet-headed Blackbirds nests and Brown-and-yellow Marshbirds nests built on marshes at any stage ($\chi^2_1 = 0.03$, $P > 0.05$ for laying; $\chi^2_1 = 0.05$, $P > 0.05$ for incubation; and $\chi^2_1 = 0.23$, $P > 0.05$ for nestling; Fig. 2A). However, nesting success (measured as the product of the nest survival for each stage) was higher for Scarlet-headed Blackbird's nests than for Brown-and-yellow Marshbird nests ($\chi^2_1 = 4.81$, $P = 0.03$; Fig. 2B). Considering a clutch size of 3 eggs, an incubation period of 13 days and a nestling period of 12 days for Scarlet-headed Blackbird's nests, the probability of a nest surviving the entire nesting cycle was 0.25. Similarly, for Brown-and-yellow Marshbird's nests with a laying period of 4.6 days, a 13 days of incubation, and a 12 days of nestling period, the nest survival probability was 0.11. Because we did not detect differences in daily nest mortality rates for any stage of the nest-

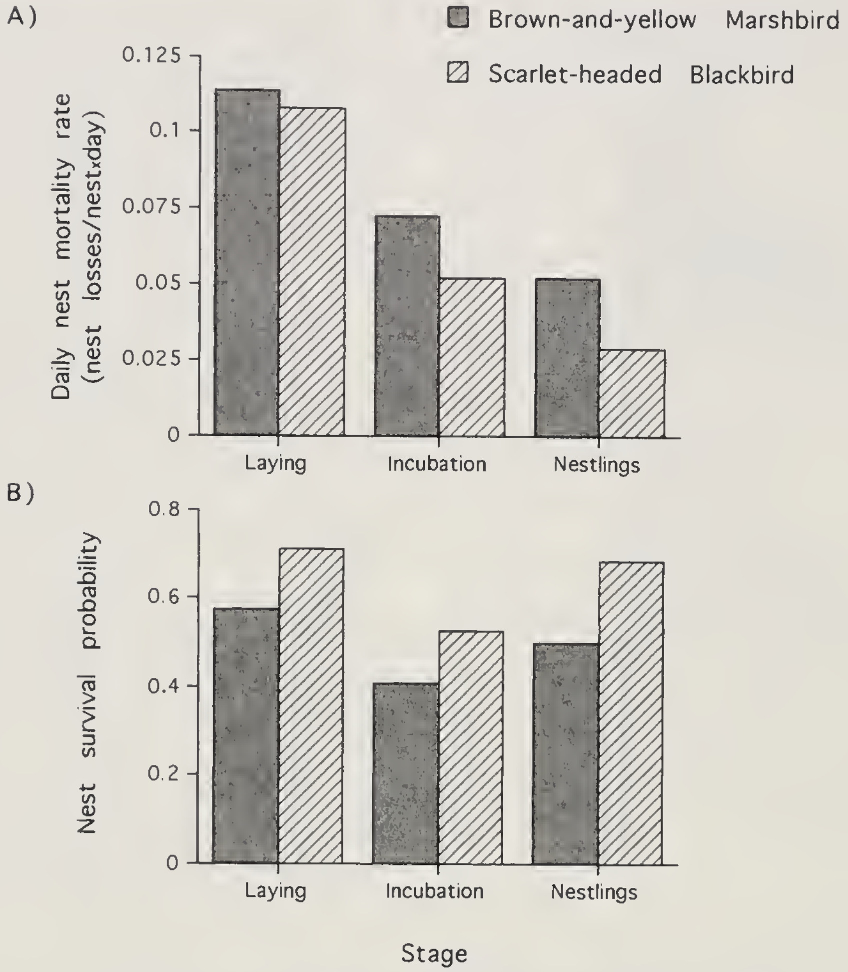

FIG. 2. A. Daily nest mortality rates estimated by Mayfield method (DNMR = nests losses/nest.day). B. Nest survival probability at laying, incubation, and nestling stages of the Brown-and-yellow Marshbird and the Scarlet-headed Blackbird nests. Nesting survival probability were estimated as $(1 - \text{DNMR})^t$, where t is the time involved on each nesting stage.

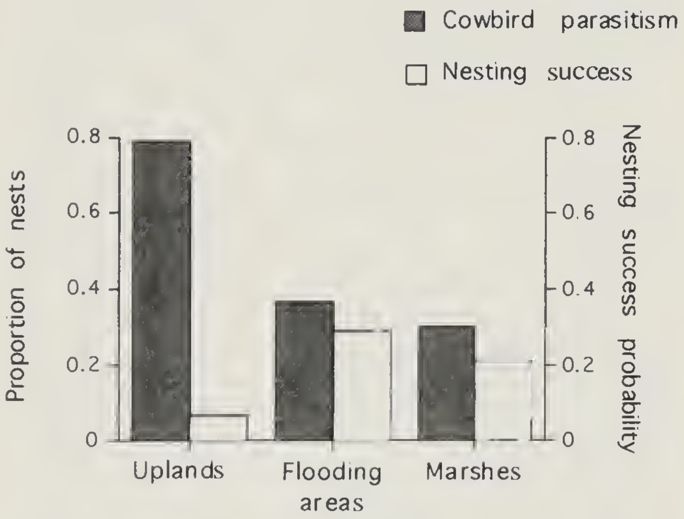

FIG. 3. Proportion of nests parasitized by cowbirds (shaded bars) and nesting success (open bars) of Brown-and-yellow Marshbird nests built in different habitats. Nesting success was estimated as the product of nest survival at each nesting stage $[(1 - DNMR)^t$, with t being the time involved on each nesting stage and $DNMR$ the respective daily mortality rate].

ing cycle, we assumed that this difference in the nest survival probability was the result of a longer laying period for the Brown-and-yellow Marshbird. When we recalculated nest survival probabilities for a 3 egg laying period, expected nest losses were similar to those of the Scarlet-headed Blackbird (nest survival probability 0.25 vs 0.14, respectively; $\chi^2_1 = 2.34$, $P > 0.05$).

We detected differences in the nesting success of Brown-and-yellow Marshbirds related to nest-site ($\chi^2_2 = 7.88$, $P = 0.02$). Nests built on flooding areas and marshes had a lower daily nest mortality rates than nests built on upland areas ($\chi^2_1 = 4.82$, $P = 0.03$; Fig. 3). When analyzed by nesting stages, no differences were found ($\chi^2_1 = 0.27$, $P \geq 0.05$, for laying; $\chi^2_1 = 3.73$, $P > 0.05$, for incubation; and $\chi^2_1 = 4.89$, $P > 0.05$, for nestling stage).

Nest attentiveness.—The Brown-and-yellow Marshbird's nest attentiveness increased over the nesting cycle (Homogeneity G-test:

$G_2 = 6.6$, $P = 0.03$). During the laying and incubation stages, 71.3% of the time at least one parent remained near the nest ($n = 87$ observations) and increased to 87.1% ($n = 62$ observations) after the chicks hatched (Homogeneity G-test: $G_1 = 6.52$, $P = 0.01$). We detected differences in nest attentiveness at any stage related to the nest habitat (Homogeneity G-test: 2 df, $P > 0.05$ for all comparisons).

Neither was there any difference in nest attentiveness by the Scarlet-headed Blackbird among different nesting stages (Homogeneity G-test: $G_2 = 0.04$, $P > 0.05$). At least one parent was near the nest on 93.2% of the visits during laying and incubation ($n = 74$) and on 92.4% of the visits during chick rearing stage ($n = 66$). Furthermore, Scarlet-headed Blackbirds were significantly more attentive to the nest during both egg laying and incubation than Brown-and-yellow Marsbirds (Homogeneity G-test: $G_1 = 5.85$, $P = 0.01$; $G_1 = 7.65$, $P = 0.006$ respectively). However, their nest attentiveness were similar during chick rearing (Homogeneity G-test: $G_1 = 1$, $P > 0.05$).

Egg survival, hatching, and fledging success.—Twenty-four Scarlet-headed Blackbird nests hatched but six were depredated at hatching. Of the 18 surviving nests, 16 produced fledglings (one produced one cowbird and one host chick) and the fates of the other 2 were unknown.

Forty-six Brown-and-yellow Marshbird nests had nestlings and 22 of these nests fledged young. Of the nests with nestlings, 18 were depredated or deserted, and we did not know the fate of the 6 remaining nests.

Egg survival was higher in Scarlet-headed Blackbird than in Brown-and-yellow Marshbird nests (Mann-Whitney test: $Z = 3.74$, $n_1 = 19$, $n_2 = 22$, $P < 0.001$). About 94.7% (± 3.8, $n = 19$) of the eggs survived in Scarlet-headed Blackbird nests whereas 74.8% (±6.4, $n = 22$) of the eggs survived the incubation period in Brown-and-yellow Marshbird nests. Hatching success was also higher in Scarlet-headed Blackbird nests (Mann-Whitney test: $Z = 3.63$, $n_1 = 18$, $n_2 = 28$, $P < 0.001$). Hatching success averaged 0.94 ± 0.04 chick/egg ($n = 18$); whereas Brown-and-yellow Marshbird hatching success averaged 0.59 ± 0.06 ($n = 28$). Fledging success was similar for both species (0.82 ± 0.06, $n = 14$, for Scarlet-headed Blackbirds, and 0.84 ± 0.07, $n = 20$, for Brown-and-yellow Marshbirds; Mann-Whitney test: $Z = 0.82$, $P > 0.05$). Differences in egg survival and hatching success resulted in fewer Brown-and-yellow Marshbirds nestlings (Mann-Whitney test: $Z = 2.94$, $n_1 = 18$, $n_2 = 28$, $P = 0.003$) in spite of their larger clutch size, but a similar number of fledglings produced per successful nest (Mann-Whitney test: $n_1 = 14$, $n_2 = 20$, $Z = 0.96$, $P > 0.05$, Fig. 4). Taking into account total nest losses, Scarlet-headed Blackbirds had a higher breeding success per egg than Brown-and-yellow Marshbirds. For all nests pooled that were found at laying and early incubation for each species, only 8.3% (28/337) of the eggs laid by Brown-and-yellow Marshbird produced fledglings, but 30.8% (29/94) of Scarlet-headed Blackbird's eggs fledged (Homogeneity G-test: $G_1 = 27.6$, $P < 0.001$). No differences were detected in brood reduction frequency between the study species where 2 or more chicks had hatched (Fisher Exact test: $P = 0.14$). Scarlet-headed Blackbirds suffered brood reduction on 50% of their nests (6/12 nests), but Brown-and-yellow Marshbirds suffered chick loss on 22.7% of the nests (5/22 nests).

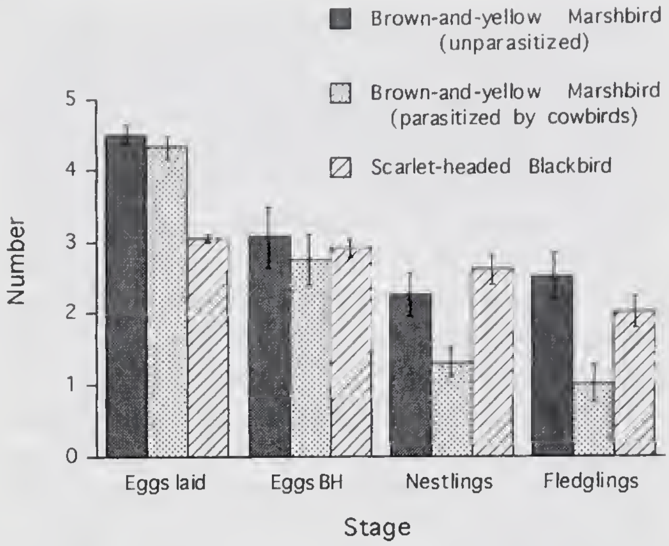

FIG. 4. Number (mean ± SEM) of eggs laid, eggs present before hatching (eggs BH), nestlings hatched, and fledglings produced in Brown-and-yellow Marshbird and Scarlet-headed Blackbird nests. In the Brown-and-yellow Marshbird, dark bars represent unparasitized nests and stippled bars indicate parasitized nests.

Missing eggs and hatching failures we observed in Brown-and-yellow Marshbird nests may be attributed to high cowbird parasitism.

Thus, we repeated the analysis excluding parasitized nests. Taking into account only unparasitized nests, egg survival was similar in Scarlet-headed Blackbird and Brown-and-yellow Marshbird nests (0.94 ± 0.04, $n = 18$, and 0.89 ± 0.06 %, $n = 9$ respectively; Mann-Whitney test: $Z = 1.21$, $P > 0.05$). Nevertheless, hatching success was higher in Scarlet-headed Blackbird nests (0.94 ± 0.04 chick/egg, $n = 17$ vs 0.73 ± 0.08 chick/egg, $n = 13$ for Brown-and-yellow Marshbirds; Mann-Whitney test: $Z = 2.65$, $P = 0.008$). On the other hand, fledging success was similar for both species (0.86 ± 0.06, $n = 13$ for Scarlet-headed Blackbirds, 0.92 ± 0.06, $n = 10$ for Brown-and-yellow Marshbirds; Mann-Whitney test, $Z = 0.8$, $P > 0.05$). Consequently, even when taking into account the higher brood parasitism it suffered, Brown-and-yellow Marshbirds produced a similar number of nestlings and fledglings per nest as did Scarlet-headed Blackbirds (Mann-Whitney test: $Z = 0.11$, $n_1 = 17$, $n_2 = 13$, $P > 0.05$ and $Z > 0.05$, $n_1 = 13$, $n_2 = 10$, $P > 0.05$, respectively; Fig. 4).

Cowbird brood parasitism.—Only 6 out of 39 (15.4%) of the Scarlet-headed Blackbird nests with completed clutches were parasitized by Shiny Cowbirds. Of these, only one fledged a cowbird. Seventy-seven of 123 Brown-and-yellow Marshbird nests that remained active for at least three days during egg laying were parasitized (62.6%). Fifty-six nests were parasitized with Shiny Cowbird eggs only (45.5 %) and 9 were parasitized with Screaming Cowbird eggs (7.3%). The remaining 12 nests (9.7%) were parasitized by both cowbird species. Of the 77 parasitized nests, 21 hatched cowbird chicks (14 only by Shiny Cowbirds, 4 only by Screaming Cowbirds, 3 by both). Cowbird fledglings were successfully reared in at least 6 nests.

Incidence of cowbird parasitism varied among habitats containing the Brown-and-yellow Marshbird nests. Nests built on uplands (thistles) suffered higher cowbird parasitism than nests built in marshes and flooding areas (Homogeneity G-test: $G_2 = 26.1$, $P < 0.001$; Fig. 3). However, Brown-and-yellow Marshbird nests in marshes and flooding areas were more heavily parasitized than Scarlet-headed Blackbird nests (Homogeneity G-test: $G_1 = 5.72$, $P = 0.02$).

When we compared parasitized and unparasitized nests of Brown-and-yellow Marshbirds, we found nearly significant differences in egg survival (0.89 ± 0.06, $n = 9$ for unparasitized nests; 0.65 ± 0.09, $n = 13$, for parasitized nests; Mann-Whitney test: $Z = 1.9$, $P = 0.052$). The number of eggs that remained at hatching did not differ between parasitized and unparasitized nests (Mann-Whitney test: $Z = 1.75$, $P > 0.05$; Fig. 4). Hatching success was higher in unparasitized than in parasitized nests (0.73 ± 0.08, $n = 13$, and 0.47 ± 0.09, $n = 15$, respectively; Mann-Whitney test: $Z = 2.08$, $P = 0.04$) resulting in more nestlings (Mann-Whitney test: $Z = 2.56$, $P = 0.01$; Fig. 4). However, fledging success was similar in parasitized and unparasitized nests (0.78 ± 0.13, $n = 10$, and 0.92 ± 0.06, $n = 10$, respectively Mann-Whitney test: $Z = 0.65$, $P > 0.05$). Overall, unparasitized nests produced more fledglings than parasitized nests (Mann-Whitney test: $Z = 2.52$, $P = 0.01$; Fig. 4). Frequency of brood reduction in parasitized and unparasitized Brown-and-yellow Marshbird's nests where 2 or more chicks hatched was similar (Fisher Exact test: $P > 0.99$). Unparasitized nests suffered brood reduction of 28.6% of their nests (2/7 nests), whereas parasitized nests suffered chick loss of 20% of the nests (3/15 nests).

DISCUSSION

Nest survival and cowbird parasitism.—About 20–25% of the nesting attempts by Brown-and-yellow Marshbirds and Scarlet-headed Blackbirds were neither depredated nor abandoned despite differences in their breeding systems. Territorial defense and higher nest attention in the Scarlet-headed Blackbird apparently do not improve the nesting success of this species compared to the Brown-and-yellow Marshbird. On the other hand, compared to Scarlet-headed Blackbird, non-territorial nesting and cooperative defense against potential predators in Brown-yellow Marshbirds apparently is not an effective strategy for reducing nest predation. The nest losses we observed were similar to those previously reported for the nesting success of the Brown-and-yellow Marshbird (Mermoz and Reboreda 1998) and the Yellow-winged Blackbird (*Agelaius thilius*; Massoni and Reboreda 1998), another sympatric marshbird species nesting in the same area. All are monogamous, but Brown-and-yellow Marshbirds and Yellow-winged Blackbirds are not territorial. In these two species males guard their mates when away from the nest, leaving the nest unattended most of the time, especially during egg laying (Mermoz 1996, this study). We found no clear relationship between the nests' spacing pattern or territorial defense and predation rate.

Cowbird parasitism was significantly higher in Brown-and-yellow Marshbirds. More than 60% of their nests were parasitized (by Shiny Cowbirds and/or Screaming Cowbirds) compared to less than 15% parasitism by Shiny Cowbirds in the Scarlet-headed Blackbird nests.

Selection of nesting sites appears to affect breeding success and cowbird parasitism rates of Brown-and-yellow Marshbirds. Comparative studies on the reproductive success of coexisting blackbirds have shown that marsh nesting birds usually experience lower nest predation rates than those in adjacent upland habitats (Case and Hewitt 1963, Robertson 1972, Picman 1988; but see Ricklefs 1969). We also found that success of Brown-and-yellow Marshbirds nesting on thistles (uplands) was lower than those nesting in marshes and flooded areas. Furthermore, nests on thistles suffer a higher cowbird parasitism and subsequently greater hatching failure, resulting in fewer fledglings per nest. A similar site effect was detected previously. In a 3-year study, Mermoz and Reboreda (1998) found that nests built in flooded areas were likely to be about 3 times more successful than those built in the uplands and suffered lower cowbird parasitism. They suggested that these differences in nest predation and cowbird parasitism could be the result of the differential distribution of plants (Mermoz and Reboreda 1998). Thistles usually grow as hedges along the sides of unpaved roads. Therefore, nests built on these plants could be detected easily by cowbirds and predators that travel along roads (Camp and Best 1994). Nests built on upland areas are vulnerable to terrestrial predators like skunks, ferrets, and rodents, which rarely could depredate nests built on flooded areas or marshes. However, Brown-and-yellow Marshbirds nest preferentially on uplands near the marshes, about 60% of the nests were built on thistles along the roads. Because similar differences on nesting success related to nest site were consistently found between Mermoz and Reboreda (1998) and our study, it is unlikely that variation in nesting success among years could explain this nesting site preference (Hatchwell et al. 1999). Further, Brown-and-yellow Marshbirds are apparently unconstrained in their choice of suitable nesting sites because they are not territorial and more than 60% of the study area is vegetated marshes. It is possible that nest building in unsuccessful sites might be maintained by gene flow (Hatchwell et al. 1999). Because we have no data about nesting success of Brown-and-yellow Marshbird elsewhere, we could not dismiss that possibility.

Instead of the nest site effect, we found that cowbird parasitism was higher in Brown-and-yellow Marshbird nests built on flooding areas and marshes than in Scarlet-headed Blackbird nests. It has been suggested that high nest attentiveness and interspecific territorial defense performed by Scarlet-headed Blackbird may preclude nests from being parasitized. In turn, mate guarding during most of the nesting cycle (mainly during the egg laying stage) in the Brown-and-yellow Marshbird could increase the chances of being parasitized (Mermoz 1996, Mermoz and Fernández 1999).

Most researchers recorded the highest nest mortality during the nestling stage, attributing it to the higher frequency of visits by adults delivering food and to the sounds of nestlings begging (Skutch 1949, Nice 1957, Young 1963, Robertson 1972, Redondo and Castro 1992, Schaub et al. 1992). A few researchers found the highest nest mortality during the laying and incubation stages (Roseberry and Klimstra 1970, Caccamise 1976, Best and Stauffer 1980, Roper and Goldstein 1997, Mermoz and Reboreda 1998). This could be attributed to increased nest defense and nest attention by the parents through the nesting cycle (Caccamise 1976, Andersson et al. 1980). However, despite the increased time parents spend near the nest throughout the nesting cycle in Brown-and-yellow Marshbirds, we were unable to find differences in nesting survival among nesting stages. Nevertheless, in a previous study on this species, a pattern of increasing nest-survival over the nesting cycle was found (Mermoz and Reboreda 1998). Consequently, the increase of parental attention to the nest could reduce the nest predation risk. On the other hand, Scarlet-headed Blackbirds were more attentive to their nests than the Brown-and-yellow Marshbirds during the egg-stage (laying and incubation), but this behavior did not increase the daily survival of their nests. The high nest mortality observed in these species appears to indicate that nest attention might not be enough to drive all potential predators away.

Helpers at the nest could contribute to nest survival mostly during the chick rearing stage by serving as sentinels or by mobbing potential predators (Orians et al. 1977, Mermoz 1996, Poiani and Pagel 1997). However, the cooperative chick rearing system in the Brown-and-yellow Marshbird does not seem to enhance nest or chick survival relative to the non-cooperative Scarlet-headed Blackbird. Helping at the nest may be only compensating for predation risk, as was found in other comparative studies (Koenig 1982, Poiani and Pagel 1997).

Clutch size, hatching and fledging success.—Brown-and-yellow Marshbirds have a larger clutch size than Scarlet-headed Blackbird. Eggs within Brown-and-yellow Marshbirds' clutches were more similar in sizes, color, and marking pattern than eggs of different clutches. Consequently, we discard the idea that their larger clutch size was the consequence of more than one female (e.g., a helper) was laying in the nest. Thus, in spite of the higher clutch size of the Brown-and yellow Marshbird (4–5 eggs vs 3 eggs for the Scarlet-headed Blackbird), hatchability was higher in the Scarlet-headed Blackbird. As a result, both species produced similar numbers of fledglings. This result could be attributable to the higher cowbird parasitism found in Brown-and-yellow Marshbird nests. In this species, cowbird parasitism effectively reduced the number of eggs hatched and chicks fledged. Cowbird eggs hatched earlier than Brown-and-yellow Marshbird eggs, and therefore the female discontinued incubation earlier thus reducing the hatching success of the eggs. Frequently cowbird chicks also could outcompete the host chicks (Mermoz and Reboreda 1994, Mermoz 1996). However, when we omitted parasitized nests from the analysis, the Scarlet-headed Blackbird showed higher hatching success than the Brown-and-yellow Marshbird. Shiny and Screaming cowbirds peck host eggs and some of their egg-pecking behavior occurs in unparasitized nests (Fraga 1998, Massoni and Reboreda 1998). Therefore, we could not dismiss the possibility that at least some of the differences in egg survival and hatching success found between Scarlet-headed Blackbirds and Brown-and-yellow Marshbirds continue to be attributable to the differences in cowbird parasitism. If cowbird egg pecking activities in unparasitized nests are negligible, differences found between the two species could be the consequence of some other phenomenon, perhaps the social complexity of their reproductive strategy. It has been suggested that in cooperative bird species, more social interactions could reduce the female's nest attentiveness and so, egg incubation efficiency (Koenig 1982). The Brown-and-yellow Marshbird could be wasting its reproductive effort because of the greater egg losses suffered during laying and incubation, and the lower hatching success of the remaining eggs. Hence, the cooperative Brown-and-yellow Marshbird and the non-cooperative, territorial Scarlet-headed Blackbird had a similar nesting success and produced the same number of fledglings. Because we have no data on adult survival, we cannot discard the possibility that the benefits of the presence of helpers in the Brown-and-yellow Marshbird increased parental lifetime fitness by reducing parental costs during breeding. Further studies on the role of food limitation in these species and the role of helpers in the Brown-and-yellow Marshbird seem to be necessary to understand the evolution of their life history strategies.

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EFFECTS OF WINTER MARSH BURNING ON ABUNDANCE AND NESTING ACTIVITY OF LOUISIANA SEASIDE SPARROWS IN THE GULF COAST CHENIER PLAIN

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ABSTRACT.—Louisiana Seaside Sparrows (*Ammodramus maritimus fisheri*) breed and winter exclusively in brackish and saline marshes along the northern Gulf of Mexico. Many Gulf Coast marshes, particularly in the Chenier Plain of southwestern Louisiana and southeastern Texas, are burned intentionally in fall or winter as part of waterfowl management programs. Fire reportedly has negatively affected two Seaside Sparrow subspecies (*A. m. nigrescens* and *A. m. mirabilis*) in Florida, but there is no published information regarding effects of fire on *A. m. fisheri.* We compared abundance of territorial male Louisiana Seaside Sparrows, number of nesting activity indicators, and vegetation structure in paired burned and unburned plots in Chenier Plain marshes in southwestern Louisiana during the 1996 breeding season (April–July) before experimental winter burns (January 1997) and again during two breeding seasons post-burn (1997–1998). We found that abundance of male sparrows decreased in burned plots during the first breeding season post-burn, but was higher than that of unburned plots during the second breeding season post-burn. Indicators of nesting activity showed a similar but non-significant pattern in response to burning. Sparrow abundance and nesting activity seemingly are linked to dead vegetation cover, which was lower in burned plots during the first breeding season post-burn, but did not differ from that in unburned plots during the second breeding season post-burn. We recommend that marsh management plans in the Gulf Coast Chenier Plain integrate waterfowl and Seaside Sparrow management by maintaining a mosaic of burned and unburned marshes and allowing vegetation to recover for at least two growing seasons before reburning a marsh. *Received 16 Sept. 1999, accepted 10 April 2000.*

The Seaside Sparrow (*Ammodramus maritimus*) breeds and winters exclusively in coastal brackish and saline marshes along the Atlantic and Gulf coasts of the United States (Robbins 1983, Post and Greenlaw 1994). This species presently is considered a "nongame migratory species of management concern" throughout much of its breeding range because of habitat loss and alteration (Greenlaw 1992). Two non-migratory subspecies, the Dusky Seaside Sparrow (*A. m. nigrescens*) and Smyrna Seaside Sparrow (*A. m. pelonata*), were sensitive to human-induced habitat changes and now are extinct (Post and Greenlaw 1994). Coastal marsh loss and degradation have been dramatic in recent years, particularly in the Gulf Coast region (Boesch et al. 1983, Alexander et al. 1986, Cowan et al. 1988). Information regarding responses of Seaside Sparrow subspecies to habitat alteration is necessary to properly manage and maintain suitable habitat for this endemic coastal marsh bird.

Louisiana Seaside Sparrows (*A. m. fisheri*), the most widely distributed non-migratory subspecies, inhabit coastal marshes from western Florida to southeastern Texas (Robbins 1983, Post and Greenlaw 1994). The year-round distribution includes the Gulf Coast Chenier Plain, a narrow 1295 km^2 band of coastal marsh extending from Vermilion Bay, Louisiana to East Bay, Texas (Gosselink 1979, Robbins 1983, Post and Greenlaw 1994). Lightning fires occur frequently in these marshes, usually between June and August (Lynch 1941). In addition, marsh managers in this region commonly use fall or winter burns to alter plant communities and promote food plants preferred by muskrats (*Odantra zibethicus*) and waterfowl (Nyman and Chabreck 1995).

Lightning and human ignited fires reportedly have been both detrimental and beneficial to two non-migratory Seaside Sparrow subspecies. The number of singing Dusky Seaside Sparrow males was reduced by half in the breeding season immediately following two extensive wildfires in a single winter as the result of a lack of suitable cover and direct

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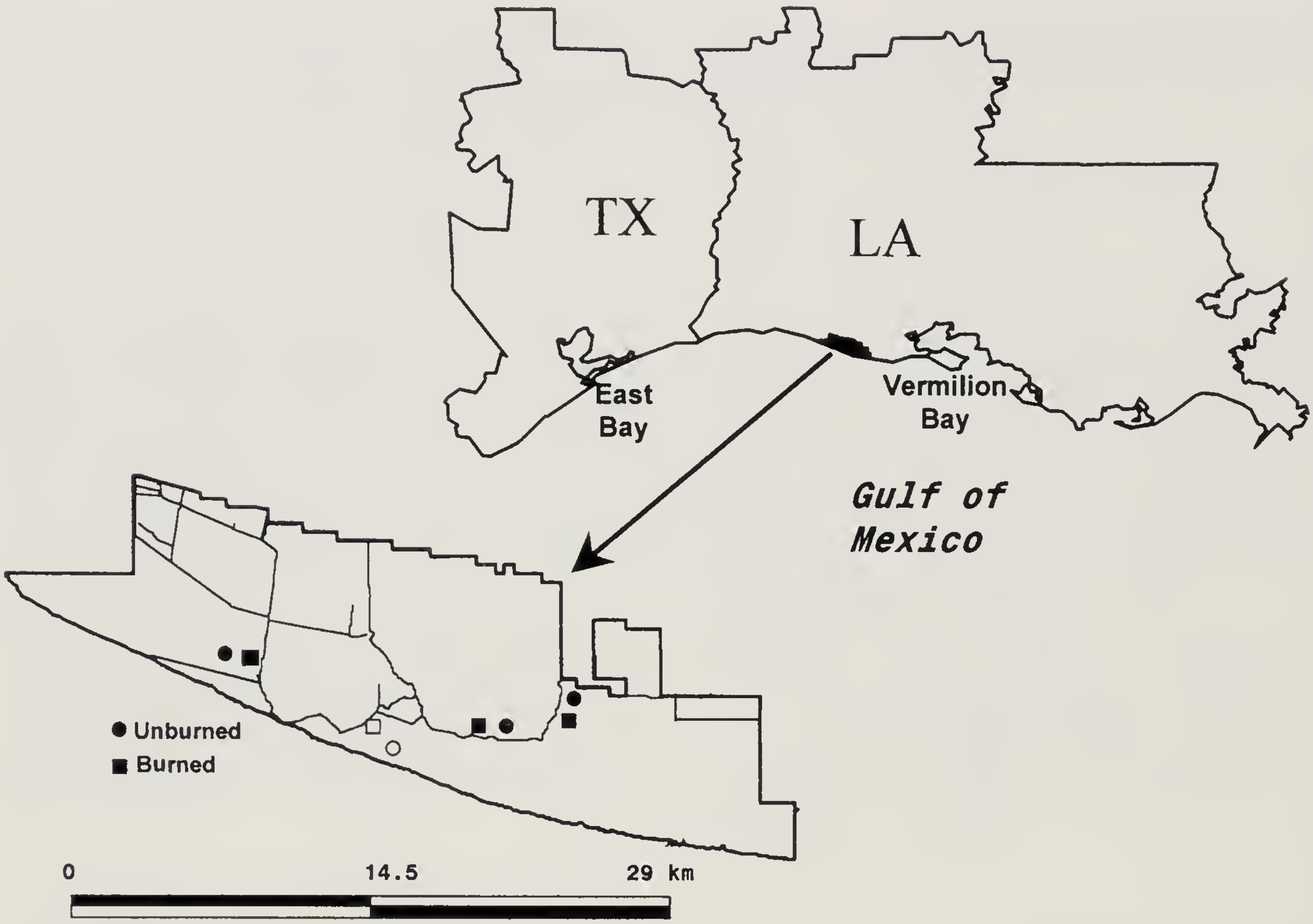

FIG. 1. Map of southern Louisiana and southeastern Texas showing locations of Rockefeller State Wildlife Refuge and four pairs of burned and unburned plots. Solid lines within the refuge boundary represent major levees. Solid and empty symbols indicate plots in brackish and saline marsh, respectively. Squares represent plots burned in January 1997; circles represent unburned plots.

mortality (Baker 1973, 1978; Walters 1992). In contrast, Sykes (1980) argued that fire was essential in maintaining Dusky Seaside Sparrow habitat because it removed woody vegetation and decreased vegetation density. Frequent human induced fires have been cited as a major threat to Cape Sable Seaside Sparrows (*A. m. mirabilis*) in southern Florida (Kushlan and Bass 1983). Cape Sable Seaside Sparrows generally were absent from marshes burned during the previous winter (Taylor 1983). Density of this subspecies, however, increased between two and four years post-burn and then declined, suggesting that periodic fire is necessary to maintain suitable habitat (Taylor 1983, Post and Greenlaw 1994). Effects of management burns on Louisiana Seaside Sparrows are unknown but could be significant, given the apparent vulnerability of several subspecies to habitat alteration. We compared abundance of territorial male Louisiana Seaside Sparrows, number of nesting activity indicators, and vegetation structure in paired burned and unburned plots in Chenier Plain marshes in southwestern Louisiana during the 1996 breeding season (April–July) before experimental winter burns (January 1997) and again during two breeding seasons post-burn (1997–1998). We predicted that responses of Louisiana Seaside Sparrows to winter burning would be similar to that of Cape Sable Seaside Sparrows (Taylor 1983); that is, the abundance of male Louisiana Seaside Sparrows and nesting activity in burned marshes would be lower than those in unburned marshes during the first breeding season after the burn, but these parameters would be equal to or greater in burned marshes than in unburned marshes in the second breeding season.

METHODS

Study area.—We chose Rockefeller State Wildlife Refuge (SWR) in southwestern Louisiana as a representative area within the Gulf Coast Chenier Plain (Fig. 1). Rockefeller SWR (headquarters coordinates: 29° 40′ N, 92° 48′ W) is a 30,700 ha area managed primarily as winter waterfowl habitat by the Louisiana

Department of Wildlife and Fisheries. Rockefeller SWR consists of 17 impoundments ranging in size from 200 to more than 4000 ha (Wicker et al. 1983) and approximately 11,700 ha of tidally influenced unimpounded marshes. Most impoundments were constructed during the late 1950s and are separated by a network of canals. Management burns on Rockefeller SWR are conducted on a 3 year rotation, with approximately one-third of the refuge area burned during a single fall/winter (October–February). Lightning-ignited fires occur on Rockefeller SWR from June–August (0–3 fires/year during 1993–1995; T. J. Hess, unpubl. data).

Marsh types on Rockefeller SWR include a band of saline marsh along the Gulf Coast, a band of brackish marsh further inland, and intermediate marsh still further inland (Chabreck 1970, Chabreck and Linscombe 1988). Saline marsh (salinity $\geq$ 10 ppt) is dominated by *Spartina alterniflora, S. patens,* and *Distichlis spicata.* Brackish marsh (5–10 ppt) is characterized by *S. patens, D. spicata,* and *Scirpus* spp. Intermediate marsh (1–5 ppt) is dominated by *Spartina patens* (Chabreck 1970, 1972; Chabreck and Linscombe 1988). Impounded marshes in our study were brackish; unimpounded marshes were exposed to tidal action of the Gulf and were brackish or saline. We did not use intermediate or fresh (salinity $<$ 1 ppt) marshes because Louisiana Seaside Sparrows were absent from these marsh types (Gabrey 1999, Gabrey et al. 1999). Virtually all vegetation was herbaceous within our study area (Gabrey 1999).

Using vegetation-type and fire-history maps of Rockefeller SWR, we selected study sites that met the following criteria: (1) minimum area of 100 ha, (2) presence of a firebreak (bayou, canal), (3) homogeneous marsh type and fire history within the site, (4) site accessibility, and (5) absence of other research projects or physical structures potentially damaged by fire. Four sites met these criteria: two in brackish impoundments and one each in unimpounded saline and unimpounded brackish marsh (Fig. 1). At each site, we established paired 250 × 250 m plots (6.25 ha each), one on each side of the firebreak. Plots were gridded at 25-m intervals (Petersen and Best 1987). One plot at each site was chosen randomly to be burned between 9–18 January 1997; control plots remained unburned throughout the study. We collected bird and vegetation data (see below) during the 1996 breeding season (April–July) prior to burning and during two breeding seasons post-burn (1997–1998).

Sparrow surveys.—We recorded abundance of male Louisiana Seaside Sparrows in study plots using the spot-mapping method (Ralph et al. 1993). Two experienced observers conducted surveys each year with one observer present for all three years. Paired plots were surveyed simultaneously (one observer/plot). To reduce potential observer bias, observers alternated between plots at each site during consecutive sampling periods. The starting point for each survey rotated among four points (one on each side of the plot). Surveys were completed within 4 h of sunrise. In 1997 and 1998, we surveyed plots 11 times from April–July, once during every 10-day interval (International Bird Census Committee 1970). Low water levels from a severe drought in April–May 1996 prevented more frequent access to plots; consequently we surveyed plots 8 times during the 1996 breeding season, once during the first two weeks of each month and once during the last two weeks.

During each survey, the observer walked slowly along every other grid line within the plot and recorded on a field map locations and flight directions (to reduce double-counting) of all males (determined by singing or territorial behavior) encountered. We did not use spot-map locations to determine territory boundaries because (1) territory size varies temporally (Best 1975), (2) individuals were spaced closely, resulting in subjective measurements (International Bird Census Committee 1970, Best 1975), (3) off-territory feeding is common in this species (Post 1974), and (4) males often moved to only one or two perches before flying beyond plot boundaries or into vegetation (S. W. Gabrey, pers. obs.).

Nesting activity.—We used nesting activity indicators (nests, copulation events, adult birds carrying food or nesting material, or flightless juveniles) to index Louisiana Seaside Sparrow productivity because of the difficulty in locating nests in dense vegetation and concern for investigator-induced nest failure. We recorded all nesting activity observed during surveys of male sparrows. In addition, beginning in May 1996, we conducted 1 h nesting activity searches before and after each survey. The observer walked along those grid lines not used during surveys and recorded all observed nesting activity. We plotted locations of nesting activity on field maps to avoid double counting.

Vegetation characteristics.—We collected vegetation data at 12 randomly selected points in each plot during the first week of June each year. We measured visual obstruction (an index to plant height) following methods described by Robel and coworkers (1970). Percent total vegetation cover (all plant species combined) and percent dead vegetation cover at each point were determined by laying a 1 m pole marked at 0.1 m intervals on the ground, and determining the percent of the pole covered (Chabreck et al. 1985). Cover classes were 7 (76–100%), 6 (51–75%), 5 (26–50%), 4 (6–25%), 3 (1–5%), 2 (few stems), 1 (single stem), and 0 (absent; Mueller-Dambois and Ellenberg 1974). To calculate mean values for categorical data, we converted cover classes to a discrete response using the midpoint of the class [i.e., Class 7 = 87.5%, Class 6 = 62.5%, Class 5 = 37.5%, Class 4 = 15%, Class 3 = 2.5%, and Classes 1 and 2 = 0.5% (Agresti 1996, Pahl et al. 1997)]. Sample points located in a pond or unvegetated mud were given visual obstruction and cover scores of 0. We calculated the mean visual obstruction score, mean total cover midpoint, and mean percent dead vegetation cover midpoint for each plot.

Breeding site fidelity.—We used mist nets to capture and band Seaside Sparrows in two of the four pairs of burned-unburned plots to estimate site fidelity in response to burning. We placed 3–7 nets (6 or 12 m × 2 m × 36 mm mesh) in a line along a grid line, and 2–5 workers attempted to flush sparrows into the nets by walking towards the nets. We aged captured sparrows as adult or juvenile using plumage characteristics and sexed sparrows based on presence of a brood patch or cloacal protuberance (Pyle et al. 1991). Sparrows were fitted with an aluminum USFWS band and 1–3 colored leg bands. In 1996, we used one or two colored bands to identify age, sex, and plot where captured. In 1997, each sparrow received a unique combination of bands to facilitate individual recognition. We did not capture sparrows in 1998. We defined net-hours as the number of 6 m nets (12 m nets were counted as two nets) times the number of hours spent trapping. We recorded capture, resight, and recapture locations on field maps.

Analysis.—We analyzed pre-burn (1996) data separately from post-burn data (1997, 1998) because the first year was a pilot year in which study protocols were developed and because sampling effort differed from post-burn years (see above). For pre-burn data, we compared male Louisiana Seaside Sparrow abundance using a repeated measures analysis of variance (ANOVA) with burn treatment (burned or unburned) as the explanatory variable and survey period (1–8) as the repeated measure. We compared nesting activity indicators, visual obstruction scores, percent total vegetation cover, and percent dead vegetation cover using single-factor ANOVAs with burn treatment as the explanatory variable.

For post-burn data, we compared male Louisiana Seaside Sparrow abundance using a repeated measures analysis of variance with burn treatment as the explanatory variable, and year (1997, 1998) and survey period (1–11) as repeated measures. We analyzed post-burn nesting activity indicators and vegetation response variables (visual obstruction, percent total vegetation cover, and percent dead vegetation cover) with a model similar to that used for male sparrow abundance, except that survey period was excluded from the model.

In all analyses, we made pairwise comparisons when necessary (using the PDIFF option in the LSMEANS statement in PROC GLM; SAS Institute 1990). Because plots were located in impounded and unimpounded marshes, we included management type (impounded or unimpounded) as a block effect in all ANOVAs. We transformed [$\log_{10}(Y + 1)$] male Louisiana Seaside Sparrow abundance, nesting activity indicators, and visual obstruction scores to meet assumptions for parametric procedures (Sokal and Rohlf 1981). We report least-squares means and 95% confidence intervals as back-transformed values unless otherwise indicated. Only four sites were available at Rockefeller SWR that met our selection criteria; consequently, we set *a priori* a significance level of 0.10 because of low statistical power (Cohen 1977). Because the three vegetation characteristics represent multivariate measurements taken at a single point, we adjusted the significance level for vegetation analyses (but not sparrow analyses) by dividing the original significance level (0.10) by the number of hypotheses tested (3) for an adjusted significance level of 0.033 (Beal and Khamis 1991, Johnson and Wichern 1992). All analyses were performed with software SAS/STAT version 6 for Windows 95.

RESULTS

Pre-burn analysis.—The number of Louisiana Seaside Sparrow males observed during 1996 breeding season surveys did not differ between control plots and those randomly selected to be burned ($F_{1,47} = 0.94$, $P > 0.10$) or among survey periods ($F_{7,47} = 1.29$, $P > 0.10$). The burn × survey period interaction also was not significant ($F_{7,47} = 0.35$, $P > 0.10$). The overall mean number of male sparrows observed/survey was 11.9 (95% CI = 10.0–14.2). Number of nesting activity indicators/plot in 1996 (3.3 indicators/plot, 95% CI = 1.3–7.0) also did not differ between control plots and those randomly selected to be burned ($F_{1,5} = 0.25$, $P > 0.10$).

Visual obstruction scores ($F_{2,5} = 0.32$, $P > 0.033$; overall mean = 7.5; 95% CI = 6.0–9.3), percent total vegetation cover ($F_{2,5} = 3.70$, $P > 0.033$; overall mean = 76.6%; 95% CI = 65.8–87.5) and percent dead vegetation cover ($F_{2,5} = 1.65$, $P > 0.033$; overall mean = 80.2%; 95% CI = 69.5–91.0) during June 1996 did not differ between control plots and those randomly selected to be burned in January 1997.

Post-burn analysis.—Our initial analysis of post-burn abundance of male Louisiana Seaside Sparrows indicated a burn × survey period × year interaction ($F_{21,131} = 4.22$, $P < 0.01$). We were interested primarily in within year differences in male abundance; consequently, we conducted separate ANOVAs for 1997 and 1998 to examine burn × survey period interactions. For 1997, we detected a burn × survey period interaction ($F_{10,65} = 4.15$, $P < 0.01$). Abundance of male Louisiana Seaside Sparrows was lower in burned than in unburned control plots for the first five surveys of 1997 but similar thereafter, except for 1–10 July (Fig. 2). For 1998 data, the burn × survey period interaction was not significant ($F_{10,65} = 0.72$, $P > 0.10$); however, the burn ($F_{1,65} = 27.04$, $P < 0.01$) and period ($F_{10,65} = 2.61$, $P < 0.01$) main effects were significant. Male sparrow abundance was higher in burned (15.8 males/survey; 95% CI = 13.1–

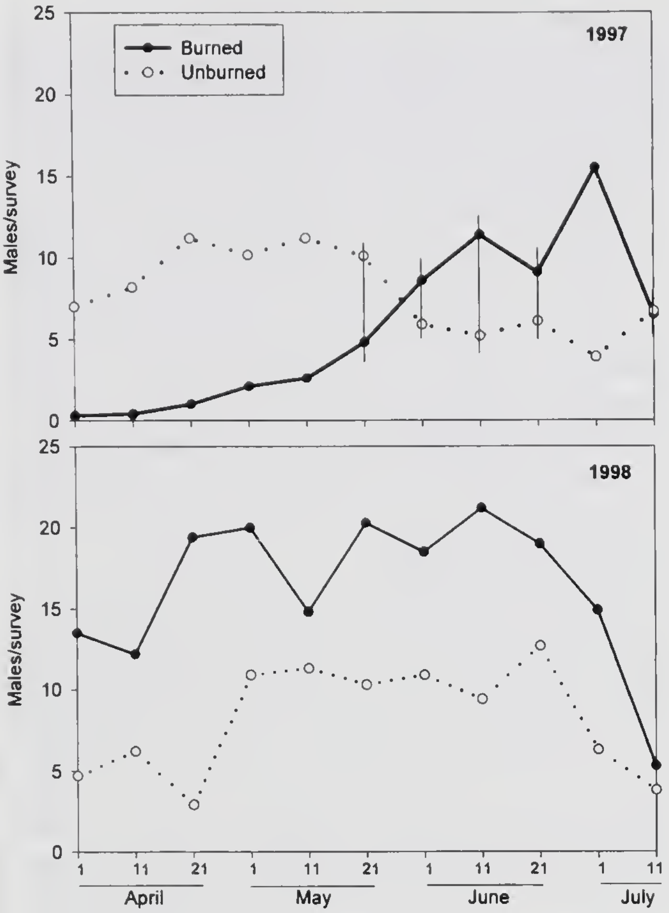

FIG. 2. Number of male Louisiana Seaside Sparrows recorded during April–July in paired burned and unburned plots on Rockefeller State Wildlife Refuge during 1997 (top) and 1998 (bottom). Experimental burns were conducted in January 1997. Points connected with vertical lines are not significantly different ($P > 0.10$).

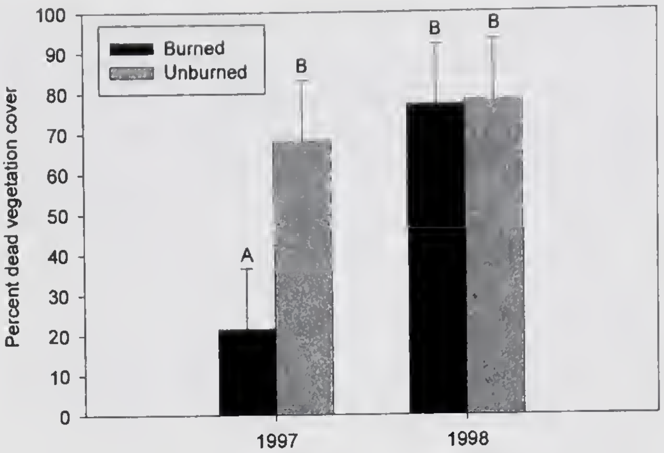

FIG. 3. Percent dead vegetation cover in paired burned and unburned plots on Rockefeller State Wildlife Refuge during June 1997–1998. Experimental burns were conducted in January 1997. Error bars represent upper 95% confidence limits. Similar letters above bars indicate that means do not differ ($P > 0.033$).

19.0) than in unburned (7.5 males/survey; 95% CI = 5.7–9.6) control plots throughout the 1998 breeding season. Male sparrow abundance generally was highest during May and June 1998 for all plots (Fig. 2).

In 1997, we recorded 2.0 (95% CI = 0.3–3.7) and 4.3 (95% CI = −1.5–10.1) nesting activity indicators/plot in burned and unburned plots, respectively. In 1998, we recorded 10.0 (95% CI = 6.5–13.5) and 8.0 (95% CI = 3.0–13.0) nesting activity indicators/plot in burned and unburned plots, respectively. The burn × year interaction ($F_{1,11} = 0.60$, $P > 0.10$) and burn main effect ($F_{1,11} = 0.02$, $P > 0.10$) were not significant. Number of nesting activity indicators/plot was higher ($F_{1,11} = 10.41$, $P < 0.01$) in 1998 (8.2 indicators/plot; 95% CI = 4.6–14.0) than in 1997 (2.1 indicators/plot; 95% CI = 0.9–4.1).

Visual obstruction scores did not differ between burn treatments ($F_{1,15} = 0.38$, $P > 0.033$) or year ($F_{1,15} = 0.55$, $P > 0.033$); the burn × year interaction also was not significant ($F_{1,15} = 0.25$, $P > 0.033$). Overall mean visual obstruction score was 7.4 (95% CI = 6.1–8.9). Percent total vegetation did not differ between burn treatments ($F_{1,15} = 0.01$, $P > 0.05$) or year ($F_{1,15} = 2.39$, $P > 0.033$); the burn × year interaction also was not significant ($F_{1,15} = 1.03$, $P > 0.033$). Overall mean percent total vegetation cover was 79.5% (95% CI = 73.3–85.7). We detected a significant year × burn interaction in the analysis of percent dead vegetation cover ($F_{1,15} = 11.44$, $P < 0.01$). In 1997, percent dead vegetation cover was lower in burned than in unburned plots but did not differ between burn treatments in 1998; percent dead vegetation cover in burned plots was lower in 1997 than in 1998 (Fig. 3).

Breeding site fidelity.—We banded 115 (73 in 1996, 42 in 1997) Seaside Sparrows during 290 net-hours in two burned and two unburned plots. We spent little time netting in burned plots in 1997 because our surveys indicated that sparrows were not present in those two plots throughout much of 1997. All encounters (resightings or recaptures) were of sparrows banded as adults and were in the plots in which they initially were caught. In 1997, we recaptured 3 of 27 adult sparrows banded in unburned plots in 1996, all within 100 m of the location of initial capture. On five occasions in 1997, we resighted at least two adult sparrows in the same unburned plots in which they had been banded in 1996. In contrast, in 1997 we resighted 1 and recaptured none of 35 adult sparrows banded in burned plots in 1996. In 1998, we resighted 7 of 38 adult sparrows banded in unburned plots in 1997; no birds banded in 1996 were encountered in unburned plots in 1998. In burned plots, however, we resighted at least one sparrow banded in 1996 on two occasions in a single burned plot but did not recapture any.

DISCUSSION

We found that none of our response variables differed between control and experimental plots during the 1996 breeding season (April–July) prior to burning in January 1997. Consequently, we assume that differences observed during the two post-burn breeding seasons (1997, 1998) primarily resulted from our experimental winter burns.

We found that abundance of male Louisiana Seaside Sparrows was reduced markedly during the first breeding season post-burn (1997) but nesting activity showed no significant decline in burned plots compared to unburned plots. We believe that Louisiana Seaside Sparrows present in our experimental plots prior to burning moved to nearby unburned marsh after the fire because (1) direct mortality of birds from fire occurred infrequently (Whelan 1995, but see Walters 1992) and (2) non-migratory populations of Seaside Sparrows stay in or near the breeding territory throughout the year and usually breed in the same territory in consecutive years (Post and Greenlaw 1994), a behavior supported by our observations of banded sparrows in unburned plots. Such displacement could affect short-term reproductive success by forcing dispersal into habitats of poorer quality, increasing population density in good quality habitats, interfering with pair bonds or mate fidelity, or delaying territory establishment or nesting activity (Best 1979, Taylor 1983).

We found that declines in male abundance and nesting activity during the first breeding season post-burn were temporary. A similar pattern of initial post-burn decline and subsequent population increase associated with plant succession was suggested for Cape Sable Seaside Sparrows (Taylor 1983). Louisiana Seaside Sparrows nest in low vegetation and may require a minimum amount of ground cover that was not attained until the second summer after burning as suggested for Vesper Sparrows (*Pooecetes gramineus*; Petersen and Best 1987). The dominant vegetation in our study area, *Spartina patens,* usually is erect in the early growth stages, but after reaching a height of about 1 m it falls over, creating a low (<1 m) closed canopy. This canopy, composed of live and dead *S. patens,* was reestablished by the second summer after burning (S. W. Gabrey, pers. obs.), coinciding with high Louisiana Seaside Sparrow abundance in burned plots.

Percent dead vegetation cover in burned plots was 50% less than in unburned plots the first breeding season after burning (1997) when Louisiana Seaside Sparrow abundance was low. In 1998, percent dead vegetation cover in burned plots recovered to pre-burn levels; this increase coincided with the increase in Louisiana Seaside Sparrow abundance. Thus, the amount of dead vegetation seemingly affects Louisiana Seaside Sparrow abundance and nesting activity in our study area. Seaside Sparrows feed primarily on invertebrates gleaned off the ground or low vegetation (Post and Greenlaw 1994); litter and dead vegetation may act as a substrate for invertebrate prey. In addition, Louisiana Seaside Sparrows use mostly dead vegetation for nest construction (S. W. Gabrey, pers. obs.); thus, burning may reduce availability of nesting material.

Sykes (1980) and Taylor (1983) emphasized the importance of properly timed fires to restore habitat for Dusky Seaside Sparrows and Cape Sable Seaside Sparrows in Florida. Our results indicate that periodic fire is an important factor affecting Louisiana Seaside Sparrow population size and nesting activity. Because one year apparently must pass before vegetation structure in burned marsh recovers to levels suitable for breeding Louisiana Seaside Sparrows, burning a marsh more frequently than every two winters will likely have detrimental effects on local sparrow populations, especially if no suitable unburned "refugia" habitat was located nearby. Consequently, we recommend that marsh managers maintain a mosaic of marshes of varying post-burn ages, including parcels of at least two years post-burn, to integrate waterfowl and Louisiana Seaside Sparrow management in Gulf Coast marshes. Local vegetation, soil characteristics, hydrology, natural fire regime, and other factors likely will determine the practicality and effectiveness of burning for Seaside Sparrow management in other parts of the breeding range.

Taylor (1983) suggested that after 5–10 years without burning, the density of dead vegetation and ground litter increases beyond suitable levels for Cape Sable Seaside Sparrows. We do not know at which point unburned marshes in the Chenier Plain will become unsuitable for Louisiana Seaside Sparrows but other studies (Gabrey 1999) suggest that sparrow abundance declined in the third year post-burn. Long-term studies of sparrow abundance and productivity would provide useful information regarding ideal burning rotations in the Chenier Plain. Comparative studies of managed burns of different frequencies or seasonality with natural lightning fires would help our understanding of the role of fire in the conservation of coastal marsh birds.

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EFFECTS OF FOREST FRAGMENTATION BY AGRICULTURE ON AVIAN COMMUNITIES IN THE SOUTHERN BOREAL MIXEDWOODS OF WESTERN CANADA

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ABSTRACT.—Little is known about the effects of forest fragmentation on bird communities in the boreal forests of western North America. Assessing the impact of forest fragmentation on bird communities has been complicated by the fact that few studies have applied statistical analyses that account for the possibility that individuals are randomly dispersed within landscapes. From 1993–1997, we contrasted bird communities in contiguous forest (54 sites) and nearby forest fragments surrounded by agricultural land (106 sites, 0.2–123 ha). Species were divided into groups based on migratory strategy (resident, short-distance migrant, long-distance migrant, and irruptive) and edge-sensitivity (edge, edge-interior, and interior). For each group, we tested whether richness and abundance were different from what would be expected if birds were distributed randomly across landscapes. Species richness was higher than expected in contiguous forest for interior species, whereas edge and short-distance migratory species were more common in the fragmented landscape. Similarly, the total abundance of interior and long-distance migratory birds was higher in contiguous forest, whereas edge birds were more abundant in the fragmented landscape. Brown Creeper (*Certhia americana*), Swainson's Thrush (*Catharus ustulatus*), Tennessee Warbler (*Vermivora peregrina*), Magnolia Warbler (*Dendroica magnolia*), Blackburnian Warbler (*Dendroica fusca*), Black-throated Green Warbler (*Dendroica virens*), and Bay-breasted Warbler (*Dendroica castanea*) were virtually absent from the fragmented landscape, yet were common in contiguous forest. Within the fragmented landscape, forest fragment size had little effect on species richness but was significantly correlated with abundance of all migratory and edge-sensitivity groups except edge and short-distance migrants. Probability of occurrence, controlling for random placement, was positively correlated with forest fragment size, percent forest cover within 5 km, or the interaction between size and cover for 19 species, most of which were associated with forest interiors. Predation and brood parasitism were higher on nests of ground and shrub nesting birds in the fragmented landscape than in contiguous forest. Fragmentation of contiguous forest in the southern boreal mixedwood zone of western Canada has a negative impact on the abundance of several resident and long-distance migratory species. *Received 23 Nov. 1999, accepted 6 May 2000.*

The effects of anthropogenic fragmentation of forests and other habitats is one of the most pressing conservation issues currently facing avian and landscape ecologists (Temple and Wilcox 1986, Robinson et al. 1995, Faaborg et al. 1998). These issues have led to numerous studies on the effects of fragment size on the composition of avian communities. Species richness and the relative abundance of interior species are often positively correlated with forest fragment size (reviewed by Walters 1998). Other patterns that are emerging in North America relate to differential effects of fragmentation depending on the migratory status of birds. In particular, long-distance migrants seem to be less common in small forest fragments than short-distance migrants or resident species (Lynch and Whigham 1984; Freemark and Merriam 1986; Askins et al. 1987, 1990; Robinson et al. 1995; Faaborg et al. 1998).

Despite the well-documented negative impacts of small fragment size on forest bird communities, the mechanisms causing this pattern remain unclear. In general, forest fragmentation seems to result in more nest predation and brood parasitism in landscapes fragmented by agriculture than in contiguous forest (Andrén 1995, Robinson et al. 1995). This has led to the suggestion that the reduced abundance or absence of species from small fragments is due to birds avoiding areas where rates of nest predation and brood parasitism are high (reviewed by Walters 1998). Increased predation or brood parasitism in small forest fragments may influence avian community structure by directly killing incubating or brooding birds, reducing recruitment through lower productivity, and/or increasing adult breeding dispersal (Haas 1998, Bayne 2000).

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That biotic processes such as nest predation are different in small versus large fragments does not necessarily demonstrate that such factors are the cause of species-area effects. Bird communities in small forest fragments may be a random sample from the regional species pool (Connor and McCoy 1979, Coleman et al. 1982, Møller 1987, Haila et al. 1993, Andrén 1996), such that species occur in fragments in proportion to the size of the fragment and the overall abundance of the species in the landscape (Freemark and Collins 1992, Hinsley et al. 1995). If birds show random dispersion, less common species should have a lower probability of occurrence in small forest fragments, and regionally abundant species should have similar abundance in most forest fragments regardless of size (Opdam et al. 1985). Clearly, determining whether species-area relationships are the result of random dispersion or are the result of non-random biotic differences, such as nest predation, is critical to avian conservation.

The objective of our study was to determine if species richness of different migratory and edge-sensitivity groups, and the abundance of individual forest bird species in different sized forest fragments in an agricultural landscape were different from what would be expected if birds were randomly distributed across the landscape. At a larger scale, we compared whether the distribution of birds was different between contiguous forest and forest fragments in an agricultural landscape, and whether nest success differed between these landscapes. We conducted this work in the southern boreal mixedwood forest of central Canada, an area with one of the highest levels of breeding avian biodiversity in North America (Robbins et al. 1989). These forests are naturally patchy because of fire, consisting of broad mosaics of stand types widely distributed across the landscape (Niemi et al. 1998). As a result of the patchy nature of the boreal forest, it has been suggested that birds breeding in the boreal forest might be able to tolerate a higher degree of fragmentation than birds in other ecosystems (Schmiegelow et al. 1996, Niemi et al. 1998). However, most work on the effects of forest fragmentation on boreal forest birds in Canada has been conducted in landscapes fragmented by industrial forestry. It remains unclear whether birds respond to fragmentation by agriculture in the same way that they respond to fragmentation caused by fire or harvesting in the boreal zone.

METHODS

Study area and site selection.—Our study was conducted in the southern boreal mixedwood zone of north-central Saskatchewan in 1993, 1995, 1996, and 1997. Point counts in contiguous forest were conducted in Prince Albert National Park (NP), a 387,500 ha protected area surrounded by agricultural land and commercial forest (53° 57′ N, 106° 22′ W). Surveys in the fragmented landscape were conducted in the rural municipality of Paddockwood (53° 31′ N, 105° 34′ W), a 135,000 ha area of privately owned land, of which 70% is used for agriculture and 25% is forest fragments (see figure in Bayne and Hobson 1997). Forests in this area are dominated by white spruce (*Picea glauca*) and trembling aspen (*Populus tremuloides*), with some black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), balsam poplar (*Populus balsamifera*), and white birch (*Betula papyrifera*). The shrub layer is variable in density and composition with beaked hazelnut (*Corylus cornuta*), red-osier dogwood (*Cornus stolonifera*), green alder (*Alnus crispa*), and white spruce saplings the most common shrub species. Fire was the dominant disturbance regime in this area, with a presettlement fire interval of approximately 30 years. Subsequent fire suppression has since increased this interval to about 200 years (J. Weir, pers. comm.).

Sites were selected from 1:12,500 air photo maps based on their tree composition, age, isolation, shape, lack of disturbance (e.g., cattle grazing or selective timber harvest), and size. Sites were pure aspen, aspen-spruce mixedwoods, or pure white spruce stands. Approximately equal numbers of sampling stations were surveyed in each forest type and fragment size. All stands we surveyed were older than 50 years and fragments were completely isolated from other forest fragments by a field or pasture. On average, the minimum distance between neighboring patches was 54 ± 30 m. The minimum distance between patches, as estimated by the LANDSAT imagery, was 30 m. Distance between sampled patches was at least one kilometer. Sites in the fragmented landscape ranged from 0.2–123 ha. Control sites were chosen from forest inventory maps for Prince Albert National Park and were located in upland forests similar to those surveyed in the fragmented landscape.

Survey methods and environmental attributes.—We evaluated the relative abundance of bird species in each landscape using the Indices Ponctuel d'Abondance (IPA) point count technique (Blondel et al. 1970). The number of point count stations we established at a site (i.e., forest fragment or stand in contiguous forest) depended on size and shape of the site. Stations were selected *a priori* from air photos, with the goal of maximizing the number of stations per site. All sites had a maximum of five point count stations separated by at least 250 m. In all sites larger than 3 ha, stations were at least 100 m from any anthropogenic edge. In contiguous forest, we established 223 point count stations at 54 sites, while in the fragmented landscape we surveyed 202 point count stations at 106 sites. Sampling effort was not equal among years. Of the contiguous forest sites, 31 were sampled in 1993, 8 in 1995, 5 in 1996, and 10 in 1997. In 1993, 5 sites were surveyed in the fragmented landscape, 21 in 1995, 15 in 1996, and 65 in 1997. Each site was visited in only one year.

Each station was visited twice per season, once in late May or early June and once in late June. We used two observers each year and alternated observers between visits at each site. Between 04:00 and 09:30 CST, all birds heard or seen during ten minutes were recorded within approximately 100 m of each point count station. Counts were subject to the constraint that only birds estimated to be within the forest stand or fragment of interest were recorded. At each station, the maximum number of individuals of each species from both visits was used as an index of relative abundance. We excluded raptors and species that nest in wetland habitats. For statistical analyses, we included only species detected at 5% or more of the sites. All species were used when calculating species richness. When estimating species richness, we also categorized species by migratory status (irruptives, resident, short-distance, long-distance migrants) and edge-sensitivity (edge, edge-interior, interior). While these categories were somewhat arbitrary, they are useful for making comparisons with previous studies (Whitcomb et al. 1981, Ambuel and Temple 1983, Freemark and Merriam 1986, Blake and Karr 1987, Johns 1993, McCollin 1993).

At each station, we estimated the proportion of the canopy composed of coniferous species to the nearest 10%. Based on the average site values we classified each site as either a pure aspen (<25% conifer cover), mixedwood (25 to 75% conifer), or pure white spruce stand (>75%). We used LANDSAT Thematic Mapper satellite imagery taken in 1995 by the Prairie Farm Rehabilitation Agency to determine the size of each forest fragment and the percentage of the total land area that was forested within 5 km.

From 1996 to 1999, we monitored active nests of ground and shrub nesting passerines in seven forest fragments ranging in size from 5–40 ha, and five contiguous forest plots. All sites were located within mixedwood stands. We marked each nest we located with flagging tape, approximately 10 m from the nest. Nests were checked every 3 to 4 days, more often near fledging time. During each check, we recorded the number of eggs (host and cowbird), number of nestlings, and any disturbance to the nests.

Statistical analyses.—To determine whether observed species richness and total abundance of each edge-sensitivity and migratory group was greater than expected if birds were randomly distributed, we used rarefaction to estimate the mean number of species expected in sites that contained different number of point-count stations. Rarefaction estimates the number of species expected from a given sample of point counts based on multiple random sampling of the original data (James and Rathbun 1981). In other words, we used rarefaction to determine how many more species would be expected in large sites simply because they were sampled more (i.e., had more stations) than small sites with only a couple of stations. Rarefaction estimates were calculated using the computer program EstimateS 5 (Colwell 1997). The expected number of species and total number of individuals per site as estimated by rarefaction was then subtracted from the observed number of species and total number of individuals per site, respectively. This provided an estimate of the departure from random (i.e., controlled species richness and abundance for increased sampling in larger patches).

A randomization procedure based on multiple linear regression modelling (Manly 1990) was used to determine whether the departure from random was influenced by landscape, year, forest type, and the interactions forest type × landscape, and landscape × year. The year × forest type interaction was not examined because not all stand types were sampled in each year. All variables were entered into the model simultaneously. Randomization testing was also used for sites in the fragmented landscape to determine whether the departure from random was influenced by forest fragment size, forest cover within 5 km, forest type, year, and the interaction between size and cover. The significance of the main and interactive effects in each model was determined by randomly shuffling the original data 1000 times. The number of times the randomly shuffled data had a residual sums of squares greater than the observed data was used to determine the approximate probability value (Manly 1990). When the main or interactive effects were significant at $P < 0.05$, a randomization test based on the least significant difference procedure was used to determine which groups within factors were significantly different. The strength of randomization testing is that the underlying distribution does not have to follow any particular statistical distribution, nor do the data have to fit the assumption of homoscedasticity (Manly 1990). Randomization testing was done using the program PopTools (Hood 2000).

We also compared whether individual species were more or less abundant than would be expected if birds were randomly distributed. To determine expected abundance of individual species, we calculated the average abundance per point count station from all point count stations and multiplied this by the number of stations within each site. The observed abundance was the sum of all stations within a site. We calculated the departure from random for each species by subtracting the expected abundance from the observed abundance at the site level (Hinsley et al. 1996). Each species at each site was then classified as either having more individuals than expected (classified as 1) or fewer individuals than expected (classified as 0). Sites where observed abundance − expected abundance = 0 were classified as having fewer individuals than expected.

Logistic regression modelling was used to determine whether the proportion of sites where individual species were more abundant than expected was influenced by landscape, year, forest type, forest type × landscape, and landscape × year. We also used logistic regression modelling for sites in the fragmented landscape to determine whether the departure from expected was influenced by forest fragment size, percent forest cover within 5 km, size × cover, forest type, and year. An all-possible regression procedure was employed where all combinations of the independent variables were examined. From all possible models, we selected the model that had the lowest Akaike Information Criteria (AICc) value. Models with the lowest AICc values explain the greatest amount of variation using the fewest number of variables (Burnham and Anderson 1998). AICc modelling was used instead of forwards or backwards stepwise logistic regression because these techniques can give different results depending on which parameter is entered or removed from the model first (Kleinbaum et al. 1988). When competing models had AIC values < 2, we presented the model that had the fewest variables that were significant at $P < 0.10$. Logistic regression modelling was done in SPSS Version 9.

For each landscape, we calculated nest success using the Mayfield method (Hensler and Nichols 1981). Mayfield estimates weight the importance of each nest in the analysis based on the stage the nest was discovered and the number of days that nest was observed. Daily survival rate was estimated using the 50% midway assumption, where a nest was assumed to have fledged or been destroyed half way between subsequent visits. Mayfield estimates of daily nest success were compared among landscapes using the program CONTRAST, which utilizes a modified chi-square test (Sauer and Williams 1989).

RESULTS

Comparisons between landscapes.—The departure from random was higher than expected in the fragmented landscape relative to contiguous forest for richness of all species ($P = 0.03$), edge species ($P < 0.001$), and short-distance migrant species ($P < 0.001$; Table 1). Interior species richness was higher than expected in contiguous forest relative to the fragmented landscape ($P = 0.01$). Richness of edge-interior ($P > 0.05$), resident ($P > 0.05$), long-distance ($P > 0.05$) and irruptive species ($P > 0.05$) were no different between landscapes from what would have been expected if species were distributed randomly (Table 1). Forest type influenced species richness ($P = 0.01$), with the departure from random being higher in mixedwood than in trembling aspen and intermediate in white spruce. Resident ($P = 0.01$) and irruptive species ($P < 0.001$) had higher than expected richness in white spruce and mixedwoods relative to pure aspen stands. Similarly, the departure from random was higher for edge-interior species in mixedwoods than in aspen or white spruce ($P = 0.03$). Mixedwood and white spruce stands had a higher departure from random for interior species richness than in trembling aspen. However, the interaction between forest type and landscape was significant for interior species richness ($P < 0.001$). Interior species richness was higher in contiguous forest than in the fragmented landscape for mixedwood and white spruce stands, whereas there was no difference in aspen stands. The departure from random for long-distance migrant richness was not influenced by landscape ($P > 0.05$), forest type ($P > 0.05$), or any of the two-way interactions. Year was not a significant predictor of the departure from random for species richness for any of the edge-sensitive or migratory groups.

The departure from random for total abundance was not significantly different between landscapes for all birds combined ($P > 0.05$), edge-interior ($P > 0.05$), resident ($P > 0.05$), short-distance migrants ($P > 0.05$), or irruptives ($P = 0.10$). The total abundance of edge birds was higher than expected in the fragmented landscape relative to contiguous forest ($P < 0.001$). Abundance of interior birds ($P = 0.003$) and perhaps long-distance migrants ($P = 0.07$) was higher in contiguous forest than in the fragmented landscape. However, the interaction between forest type and landscape was significant for interior species ($P = 0.02$). The abundance of interior birds was higher in contiguous forest than in the fragmented landscape for mixedwood and white spruce stands, whereas there was no difference between landscapes in aspen stands. Edge birds were more abundant than expected in aspen stands relative to mixedwood or white spruce ($P = 0.05$). Conversely, mixedwood and white spruce stands supported more interior ($P = 0.005$), resident ($P = 0.01$), and irruptive birds ($P < 0.001$) than pure aspen stands. Short-distance migrants were more abundant than expected in white spruce than mixedwoods or pure aspen ($P = 0.01$). Annual variation in abundance was observed for all birds ($P = 0.003$), edge-interior ($P = 0.02$), interior ($P = 0.003$), resident ($P =$

TABLE 1. Mean departure (least squares means) from what would be expected if birds were randomly distributed among landscapes and forest types for species richness and total abundance. Numbers in parentheses are the lower and upper bounds of the 95% confidence intervals for that estimate. Probability that departure from random was greater than expected is also given.

	Contiguous forest	Fragmented forest	*P*	Trembling aspen	Mixedwoods	White spruce	*P*
			Departure from random for species richness				
All species	−5.9 (−7.3, −4.6)	−3.1 (−4.2, −1.9)	0.03	−5.9 (−6.9, −4.9)	−3.8 (−4.9, −2.8)	−3.8 (−5.6, −1.9)	0.01
Edge	−3.2 (−4.0, −2.6)	0.9 (0.3, 1.5)	<0.001	−0.4 (−0.9, 0.0)	−1.6 (−2.1, −1.0)	−1.7 (−2.6, −0.7)	0.19
Edge-interior	−1.5 (−2.1, −0.9)	−1.4 (−1.9, −0.9)	0.19	−1.8 (−2.3, −1.4)	−0.9 (−1.4, −0.4)	−1.6 (−2.4, −0.7)	0.03
Interior	−1.2 (−2.0, −0.3)	−2.6 (−3.2, −1.9)	0.01	−3.6 (−4.2, −3.0)	−1.4 (−2.1, −0.7)	−0.5 (−1.7, 0.6)	<0.001
Resident	−0.6 (−1.2, −0.1)	−0.6 (−1.0, −0.2)	0.92	−1.3 (−1.7, −0.9)	−0.4 (−0.8, 0.1)	−0.2 (−0.9, 0.6)	0.01
Short-distance	−2.1 (−2.8, −1.4)	0.7 (0.2, 1.3)	<0.001	−1.1 (−1.6, −0.6)	−0.8 (−1.3, −0.3)	−0.2 (−1.1, 0.7)	0.56
Long-distance	−3.2 (−3.9, −2.4)	−3.0 (−3.6, −2.4)	0.67	−2.9 (−3.4, −2.3)	−2.7 (−3.3, −2.1)	−3.7 (−4.8, −2.7)	0.16
Irruptive	−0.04 (−0.3, 0.2)	−0.2 (−0.4, 0.1)	0.11	−0.6 (−0.8, −0.5)	0.1 (−0.2, 0.2)	0.3 (−0.1, 0.6)	<0.001
			Departure from random for abundance				
All species	1.2 (−4.1, 6.6)	−5.3 (−9.6, −0.9)	0.13	−5.7 (−9.5, 1.9)	−1.2 (−5.5, 3.0)	0.8 (−6.5, 8.1)	0.09
Edge	−4.7 (−6.6, −2.9)	1.4 (−0.1, 2.9)	<0.001	0.5 (−0.8, 1.8)	−2.8 (−4.3, −1.4)	−2.6 (−5.1, −0.1)	0.05
Edge-interior	−0.7 (−3.0, 1.7)	−2.3 (−4.2, −0.4)	0.68	−2.2 (−3.8, −0.5)	0.4 (−1.5, 2.2)	−2.7 (−5.8, 0.5)	0.10
Interior	6.6 (3.4, 9.8)	−4.3 (−7.0, 1.8)	0.003	−4.0 (−6.2, −1.7)	1.2 (−1.3, 3.8)	6.1 (1.7, 10.5)	0.005
Resident	0.6 (−0.6, 1.8)	−0.5 (−1.6, 0.5)	0.34	−1.9 (−2.7, −1.0)	0.7 (−0.3, 1.6)	1.3 (−0.4, 2.9)	0.01
Short-distance	0.1 (−1.7, 1.8)	1.8 (0.4, 3.2)	0.54	−1.4 (−2.6, −0.2)	0.3 (−1.1, 1.7)	3.8 (1.5, 6.2)	0.01
Long-distance	−0.5 (−3.8, 2.7)	−6.6 (−9.2, −3.9)	0.07	−0.3 (−2.6, 2.0)	−3.8 (−6.4, −1.3)	−6.5 (−10.9, −2.0)	0.54
Irruptive	1.1 (−0.2, 2.5)	0.1 (−1.1, 1.1)	0.10	−2.2 (−3.2, 1.2)	1.6 (0.5, 2.7)	2.3 (0.4, 4.1)	<0.001

0.02), long-distance ($P < 0.001$), and possibly irruptive birds ($P = 0.08$). For the most part, variation in abundance among years was consistent among landscapes. However, for edge ($P = 0.08$), interior ($P = 0.06$), and resident birds ($P = 0.07$) there was a suggestion that differences in abundance between landscapes were different between years.

In both landscapes combined, 79 bird species were detected. Many (38%) were detected at less than 5% of sites and were not analyzed individually (Table 2). A large portion (37%) of the 49 species examined did not differ in occurrence from what would have been expected if birds were randomly distributed between landscapes (Table 3). Least Flycatcher (*Empidonax minimus*), Philadelphia Vireo (*Vireo philadelphicus*), American Crow (*Corvus brachyrhynchos*), House Wren (*Troglodytes aedon*), American Robin (*Turdus migratorius*), Cedar Waxwing (*Bombycilla cedrorum*), Clay-colored Sparrow (*Spizella pallida*), Song Sparrow (*Melospiza melodia*), Brown-headed Cowbird (*Molothrus ater*), and American Goldfinch (*Carduelis tristis*) were more common than expected in the fragmented landscape (Table 2). Conversely, Yellow-bellied Sapsucker (*Sphyrapicus varius*), Pileated Woodpecker (*Dryocopus pileatus*), Gray Jay (*Perisoreus canadensis*), Brown Creeper (*Certhia americana*), Red-breasted Nuthatch (*Sitta canadensis*), Winter Wren (*Troglodytes troglodytes*), Tennessee Warbler (*Vermivora peregrina*), Magnolia Warbler (*Dendroica magnolia*), Black-throated Green Warbler (*Dendroica virens*), Bay-breasted Warbler (*Dendroica castanea*), Canada Warbler (*Wilsonia canadensis*), White-winged Crossbill (*Loxia leucoptera*), and Evening Grosbeak (*Coccothraustes vespertinus*) were significantly more common than expected in contiguous forest (Table 3).

The interaction between forest type and landscape was significant for three species. Ruby-crowned Kinglet (*Regulus calendula*) was more common in fragmented mixedwood stands than in contiguous forest ($P = 0.002$), while there was no difference between landscapes in white spruce ($P > 0.05$) or trembling aspen ($P > 0.05$). Ovenbird (*Seiurus aurocapillus*) was more common than expected in contiguous forest dominated by aspen than in aspen forest fragments ($P < 0.001$) and mixedwoods ($P = 0.007$), whereas they were always less common than expected in white spruce. Cape May Warbler (*Dendroica tigrina*) was significantly more common in white spruce stands in contiguous forest than forest fragments ($P = 0.04$), whereas there was no difference between landscapes in mixedwoods ($P > 0.05$) or trembling aspen ($P > 0.05$). Finally, Swainson's Thrush (*Catharus ustulatus*) was more common than expected in pure aspen stands in contiguous forest than in forest fragments ($P = 0.03$), whereas there was no difference in mixedwoods ($P > 0.05$) or white spruce stands ($P > 0.05$).

Half the species (51%) showed a preference for a particular forest type (Table 3). Red-eyed Vireo (*Vireo olivaceus*), Hermit Thrush (*Catharus guttatus*), Chestnut-sided Warbler (*Dendroica pensylvanica*), Black and White Warbler (*Mniotilta varia*), Ovenbird, American Redstart (*Setophaga ruticilla*), White-throated Sparrow (*Zonotrichia albicollis*), Rose-breasted Grosbeak (*Pheucticus ludovicianus*), and Brown-Headed Cowbird were more common than expected in trembling aspen stands (Table 3). In contrast, American Crow, Boreal Chickadee (*Podecile hudsonicus*), Ruby-crowned Kinglet, Cape May Warbler, Yellow-rumped Warbler (*Dendroica coronata*), Bay-breasted Warbler, Dark-eyed Junco (*Junco hyemalis*), and Pine Siskin (*Carduelis pinus*) were more common than expected in pure white spruce stands (Table 3). Blue-headed Vireo (*Vireo solitarius*), Gray Jay, Red-breasted Nuthatch, Blackburnian Warbler (*Dendroica fusca*), Black-throated Green Warbler (*Dendroica virens*), Chipping Sparrow (*Spizella passerina*), and White-winged Crossbill, and were more common than expected in white spruce and mixedwoods relative to trembling aspen (Table 3). The occurrence of 12 species was influenced by year (Table 3). However, annual variation was consistent among landscapes, as year interacted with landscape strongly for only two species (Table 3). Boreal Chickadee was significantly more common in contiguous forest in 1993 only, while Ruby-crowned Kinglet was significantly more common in forest fragments in 1995 only.

Factors influencing avian communities in the fragmented landscape.—The departure from random for species richness was not cor-

TABLE 2. Probability that the abundance of individual species was influenced by forest fragment size, forest cover within 5 km of site, forest type, and year, more than would be expected if individuals were randomly distributed. The slope of significant relationships is indicated as positive (+) or negative (−). All species detected in study area are shown.

Common name	Scientific name	Edge sensitivity[a]	Migratory strategy[b]	Size	Cover	Forest	Year	S × C
	Species more common in small fragments or areas with low local forest cover							
American Crow	*Corvus brachyrhynchos*	EI	S	NS	0.10^-	0.01	NS	NS
House Wren	*Troglodytes aedon*	E	S	NS	NS	0.06	NS	0.03^+
Ruby-crowned Kinglet	*Regulis calendula*	I	S	NS	0.03^-	0.001	NS	NS
American Robin	*Turdus migratorius*	E	S	NS	NS	NS	NS	0.09
Clay-colored Sparrow	*Spizella pallida*	E	L	0.07	0.007^-	NS	NS	0.06
Song Sparrow	*Melospiza melodia*	E	S	0.008^-	0.09^-	0.009	0.03	NS
	Species more common in large fragments or areas with high local forest cover within 5 km							
Yellow-bellied Sapsucker	*Sphyrapicus varius*	EI	S	0.01^+	NS	NS	NS	NS
Hairy Woodpecker	*Picoides villosus*	I	R	0.03^+	NS	NS	NS	NS
Black-capped Chickadee	*Podecile atricapillus*	EI	R	0.07^+	NS	NS	NS	0.04^+
Cedar Waxwing	*Bombycilla cedrorum*	E	S	0.09^+	NS	0.06	NS	NS
Chestnut-sided Warbler	*Dendroica pensylvanica*	E	L	NS	0.02^+	0.01	NS	NS
Mourning Warbler	*Oporornis philadelphia*	E	L	NS	0.07^+	NS	NS	NS
Connecticut Warbler	*Oporornis agilis*	I	L	0.009^+	NS	NS	NS	NS
Ovenbird	*Seiurus aurocapillus*	I	L	0.004^+	0.002^+	NS	NS	0.04^+
American Redstart	*Setophaga ruticilla*	I	L	0.01^+	0.001^+	0.003	NS	NS
White-throated Sparrow	*Zonotrichia albicollis*	E	S	0.03^+	NS	0.04	0.04	NS
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	EI	L	0.007^+	NS	0.05	NS	NS
Evening Grosbeak	*Coccothraustes vespertinus*	EI	Ir	0.07^+	NS	NS	NS	NS
	Species more common in large fragments with low forest cover within 5 km							
Red-breasted Nuthatch	*Sitta canadensis*	I	R	NS	0.02^-	0.007	NS	0.008^-
Cape May Warbler	*Dendroica tigrina*	I	L	NS	NS	0.02	NS	0.002^-
Yellow-rumped Warbler	*Dendroica coronata*	I	S	NS	0.04^-	0.001	NS	0.07^-
Blackburnian Warbler	*Dendroica fusca*	I	L	NS	0.01^-	0.003	NS	0.004^-
Chipping Sparrow	*Spizella passerina*	E	L	NS	0.008^-	0.03	0.02	0.03
Dark-eyed Junco	*Junco hyemalis*	E	S	NS	NS	0.002	NS	0.02^-
Pine Siskin	*Carduelis pinus*	EI	Ir	NS	0.02^-	0.01	NS	0.009^-
	Species randomly distributed within fragmented landscape							
Ruffed Grouse	*Bonasa umbellus*	EI	R	NS	NS	NS	NS	NS
Pileated Woodpecker	*Dryocopus pileatus*	EI	R	NS	NS	NS	NS	NS
Least Flycatcher	*Empidonax minimus*	E	L	NS	NS	0.05	NS	NS

TABLE 2. CONTINUED

Common name	Scientific name	Edge sensitivity[a]	Migratory strategy[b]	Size	Cover	Forest	Year	S × C
Blue-headed Vireo	*Vireo solitarius*	I	L	NS	NS	0.001	NS	NS
Red-eyed Vireo	*Vireo olivaceus*	EI	L	NS	NS	0.06	NS	NS
Philadelphia Vireo	*Vireo philadelphicus*	EI	L	NS	NS	0.05	NS	NS
Blue Jay	*Cyanocitta cristata*	EI	R	NS	NS	NS	NS	NS
Common Raven	*Corvus corax*	EI	R	NS	NS	NS	NS	NS
Boreal Chickadee	*Poecile hudsonicus*	I	R	NS	NS	NS	NS	NS
Hermit Thrush	*Catharus guttatus*	I	S	NS	NS	NS	NS	NS
Tennessee Warbler	*Vermivora peregrina*	EI	L	NS	NS	NS	NS	NS
Black-and-white Warbler	*Mniotilta varia*	I	L	NS	NS	NS	NS	NS
Yellow Warbler	*Dendroica petechia*	E	L	NS	NS	NS	NS	NS
Canada Warbler	*Wilsonia canadensis*	I	L	NS	NS	NS	NS	NS
Brown-headed Cowbird	*Molothrus ater*	E	S	NS	NS	0.003	0.08	NS
White-winged Crossbill	*Loxia leucoptera*	EI	Ir	NS	NS	NS	NS	NS
American Goldfinch	*Carduelis tristis*	E	S	NS	NS	NS	0.07	NS
Species rare in fragmented landscape and not tested statistically								
Mourning Dove	*Zenaida macroura*	E	S					
Ruby-throated Hummingbird	*Archilochus colubris*	E	L					
Northern Flicker	*Colaptes auratus*	EI	S					
Downy Woodpecker	*Picoides pubescens*	EI	R					
Three-toed Woodpecker	*Picoides tridactylus*	I	R					
Black-backed Woodpecker	*Picoides arcticus*	I	R					
Olive-sided Flycatcher	*Contopus borealis*	EI	L					
Western Wood-Peewee	*Contopus sordidulus*	EI	L					
Yellow-bellied Flycatcher	*Empidonax flaviventris*	I	L					
Alder Flycatcher	*Empidonax minimus*	E	L					
Eastern Phoebe	*Sayornis phoebe*	EI	S					
Warbling Vireo	*Vireo gilvus*	E	L					
Gray Jay	*Perisoreus canadensis*	EI	R					
Black-billed Magpie	*Pica pica*	E	R					
Tree Swallow	*Tachycineta bicolor*	EI	L					
Barn Swallow	*Hirundo rustica*	EI	S					
Brown Creeper	*Certhia americana*	I	S					
White-breasted Nuthatch	*Sitta carolinensis*	I	R					
Winter Wren	*Troglodytes troglodytes*	I	S					
Golden-crowned Kinglet	*Regulus satrapa*	I	S					

TABLE 2. CONTINUED

Common name	Scientific name	Edge sensitivity[a]	Migratory strategy[b]	Size	Cover	Forest	Year	S × C
Veery	*Catharus fuscescens*	I	L					
Swainson's Thrush	*Catharus ustulatus*	I	L					
Magnolia Warbler	*Dendroica magnolia*	I	L					
Black-throated Blue Warbler	*Dendroica caerulescens*	I	L					
Black-throated Green Warbler	*Dendroica virens*	I	L					
Bay-breasted Warbler	*Dendroica castanea*	I	L					
Wilson's Warbler	*Wilsonia pusilla*	I	L					
Northern Waterthrush	*Seiurus noveboracensis*	I	L					
Western Tanager	*Piranga ludoviciana*	I	L					
Savanna Sparrow	*Passerculus sandwichensus*	E	S					
Lincoln's Sparrow	*Melospiza lincolnii*	E	L					
Vesper Sparrow	*Pooecetes gramineus*	E	S					
Common Grackle	*Quiscalus quiscula*	E	S					
Baltimore Oriole	*Icterus galbula*	E	L					
Purple Finch	*Carpodacus purpureus*	EI	S					
Red Crossbill	*Loxia curvirostra*	I	Ir					
Pine Grosbeak	*Pinicola enucleator*	E	Ir					

[a] E = edge, I = interior, EI = edge-interior.

[b] R = resident, S = short-distance migrant, L = long-distance migrant, Ir = irruptive.

TABLE 3. Proportion of sites where departure from expected was greater than zero in each landscape and forest stand type. Results of logistic regression models for all parameters examined are also given. Parameters with NS were not selected in the model.

Species	Landscape			Forest stand type				Year	L × Y	L × F
	Forest	Fragments	*P*	TA	Mix	WS	*P*	*P*	*P*	*P*
Species more common than expected in fragmented landscape										
Least Flycatcher	9	22	0.01	26	6	6	NS	NS	NS	NS
Philadelphia Vireo	4	27	0.02	30	6	0	0.005	NS	NS	NS
American Crow	7	22	0.01	9	20	44	0.002	NS	NS	NS
House Wren	0	19	0.02	19	4	6	NS	NS	NS	NS
American Robin	6	27	0.003	24	14	17	NS	NS	NS	NS
Cedar Waxwing	11	22	0.002	15	20	28	NS	0.09	0.07	NS
Clay-colored Sparrow	0	17	0.02	9	12	22	NS	NS	NS	NS
Song Sparrow	0	43	0.004	39	8	28	NS	0.03	0.10	NS
Brown-headed Cowbird	4	40	0.001	38	12	6	0.001	0.04	NS	NS
American Goldfinch	0	35	0.002	23	18	39	NS	0.60	NS	NS
Species more common than expected in contiguous forest										
Yellow-b. Sapsucker	26	12	0.03	14	22	17	NS	0.07	NS	NS
Pileated Woodpecker	20	3	0.001	7	10	17	NS	NS	NS	NS
Gray Jay	26	3	0.001	2	26	11	0.005	NS	NS	NS
Brown Creeper	33	0	0.001	7	16	22	NS	NS	NS	NS
Red-breasted Nuthatch	35	13	0.06	10	36	33	0.002	0.05	NS	NS
Winter Wren	28	19	0.002	3	16	6	NS	NS	0.08	NS
Swainson's Thrush	46	2	0.001	7	32	28	NS	NS	NS	0.001
Tennessee Warbler	57	5	0.001	17	32	22	NS	0.05	NS	NS
Magnolia Warbler	35	1	0.001	8	18	22	NS	NS	NS	NS
Black-thr. Green Warbler	39	0	0.001	7	22	22	0.06	NS	NS	NS
Bay-breasted Warbler	33	1	0.001	2	22	33	0.001	NS	NS	NS
Canada Warbler	20	4	0.001	13	6	0	NS	NS	NS	NS
Ovenbird	61	18	NS	41	28	0	0.001	NS	NS	0.001
White-winged Crossbill	24	7	0.009	5	22	22	0.03	NS	NS	NS
Evening Grosbeak	24	3	0.001	4	18	17	NS	NS	NS	NS
Species randomly distributed among landscapes										
Ruffed Grouse	13	33	NS	28	26	17	NS	0.003	NS	NS
Hairy Woodpecker	20	7	NS	12	10	11	NS	0.03	NS	NS
Blue-headed Vireo	22	21	NS	8	36	50	0.001	0.08	NS	NS
Red-eyed Vireo	30	42	NS	50	26	11	0.002	NS	NS	NS
Blue Jay	9	15	NS	10	20	11	NS	NS	NS	NS
Common Raven	22	14	NS	14	20	22	NS	NS	NS	NS
Black-capped Chickadee	15	17	NS	15	18	17	NS	NS	NS	NS
Boreal Chickadee	20	5	NS	2	18	27	0.002	NS	0.006	NS
Ruby-crowned Kinglet	24	36	NS	13	50	78	0.001	NS	0.006	0.02
Hermit Thrush	24	22	NS	29	16	6	0.01	NS	NS	NS
Chestnut-sided Warbler	20	30	NS	41	10	0	0.002	NS	NS	NS
Cape May Warbler	26	10	NS	2	30	44	0.001	NS	NS	0.04
Yellow-rumped Warbler	37	21	NS	8	48	67	0.001	NS	NS	NS
Black-and-White Warbler	11	19	NS	24	6	6	0.02	NS	NS	NS
Blackburnian Warbler	24	18	NS	8	36	39	0.001	NS	NS	NS
Yellow Warbler	2	10	NS	12	0	0	NS	NS	NS	NS
Mourning Warbler	17	30	NS	30	24	6	NS	NS	NS	NS
Connecticut Warbler	19	14	NS	20	14	0	NS	NS	NS	NS
American Redstart	15	27	NS	39	2	0	0.004	NS	NS	NS
Chipping Sparrow	30	25	NS	13	42	50	0.002	0.005	NS	NS
White-throated Sparrow	28	19	NS	32	10	6	0.002	0.04	NS	NS
Dark-eyed Junco	7	10	NS	3	8	44	0.001	NS	NS	NS
Rose-breasted Grosbeak	20	28	NS	37	14	0	0.02	NS	NS	NS
Pine Siskin	32	15	NS	4	36	61	0.001	NS	NS	NS

related with fragment size for all species ($r = -0.01$, $P > 0.05$), edge-interior ($r = 0.18$, $P > 0.05$), interior ($r = 0.14$, $P > 0.05$), short-distance migrants ($r = -0.17$, $P > 0.05$), long-distance migrants ($r = -0.01$, $P > 0.05$), or irruptive species ($r = 0.08$, $P > 0.05$). The departure from random for edge species was negatively correlated with forest fragment size ($r = -0.27$, $P = 0.01$), while resident species were positively correlated with forest fragment size ($r = 0.22$, $P = 0.05$). The departure from random for richness of long-distance migrants was positively correlated with the proportion of forest cover within 5 km ($r = 0.22$, $P = 0.03$). Forest type had a significant influence on the departure from random for the richness of irruptives ($P < 0.001$), residents ($P = 0.02$), and interior species ($P = 0.03$). Annual variation in the departure from random was significant for richness of all species ($P < 0.001$), edge ($P < 0.001$), edge-interior ($P < 0.001$), residents ($P = 0.04$), short-distance migrants ($P = 0.04$), and long-distance migrant species ($P < 0.001$).

The departure from random for abundance was positively correlated with forest fragment size for all birds ($r = 0.58$, $P < 0.001$), edge-interior ($r = 0.47$, $P < 0.001$), interior ($r = 0.52$, $P < 0.001$), resident ($r = 0.28$, $P = 0.01$), long-distance ($r = 0.45$, $P < 0.001$), and irruptive birds ($r = 0.30$, $P = 0.02$). The departure from random for abundance of edge species ($r = 0.18$, $P > 0.05$) and short-distance migrants ($r = 0.11$, $P > 0.05$) was not correlated with forest fragment size. Long-distance migrant ($r = 0.36$, $P = 0.005$) and interior bird ($r = 0.26$, $P = 0.02$) abundance was positively correlated with the percentage of forest cover within 5 km. Annual variation in the departure from random was significant for total abundance of all species ($P < 0.001$), edge ($P < 0.001$), edge-interior ($P < 0.001$), interior ($P = 0.05$), residents ($P = 0.03$), short-distance migrants ($P = 0.004$), and long-distance migrant birds ($P < 0.001$). The type of forest influenced the departure from random for edge ($P = 0.01$), resident ($P = 0.03$), short-distance migrant ($P = 0.03$), long-distance migrant ($P < 0.001$), and irruptive birds ($P = 0.004$).

Of the 42 species examined in the fragmented landscape, 40% did not differ in abundance from what was expected if individuals were distributed randomly and showed no area or isolation sensitivity. American Crow, Ruby-crowned Kinglet, Clay-colored Sparrow, and Song Sparrow were negatively correlated with forest cover within 5 km. Clay-colored Sparrow and Song Sparrow were more common than expected in small forest fragments (Table 2). The departure from random was positively correlated with forest fragment size for Yellow-bellied Sapsucker, Hairy Woodpecker, Black-capped Chickadee (*Poecile atricapillus*), Cedar Waxwing, Connecticut Warbler (*Oporornis agilis*), Ovenbird, American Redstart, White-throated Sparrow, Rose-breasted Grosbeak, and Evening Grosbeak (Table 2). Chestnut-sided Warbler, Mourning Warbler (*Oporornis philadelphia*), Ovenbird, and American Redstart were more common in areas with higher local forest cover (Table 2). The departures from expected for Red-breasted Nuthatch, Cape May Warbler, Yellow-rumped Warbler, Blackburnian Warbler, Chipping Sparrow, Dark-eyed Junco, and Pine Siskin were significantly correlated with the interaction between size and local forest cover. All of these species were more common than expected in mature white spruce stands that were large but isolated. Year was a significant predictor of the departure from random for Chipping Sparrow, Song Sparrow, White-throated Sparrow, Brown-headed Cowbird, and American Goldfinch (Table 2). In total, 21 species showed a preference for a particular forest type in the fragmented landscape (Table 2).

Nest success.—We located 67 nests from eight species in the fragmented landscape and 56 nests from seven species in contiguous forest. The majority of nests located were Ovenbird (59%), followed by Hermit Thrush (13%), Chipping Sparrow (11%), White-throated Sparrow (7%), and a one or two nests each of Red-eyed Vireo, Tennessee Warbler, Yellow-rumped Warbler, Mourning Warbler, Connecticut Warbler, and American Redstart. Daily nest survival was significantly lower in the fragmented landscape (0.960 ± 0.007) than in contiguous forest (0.979 ± 0.005; $P = 0.02$). Cowbird parasitism was more common in the fragmented landscape where 19% of nests were parasitized whereas no nests were parasitized in contiguous forest ($\chi^2 = 18.8$, $P < 0.001$).

DISCUSSION

Species richness was higher in the fragmented landscape than in contiguous forest. The increase in species richness with fragmentation was primarily due to the addition of several short-distance migrants that were associated with edge habitats. In contrast, long-distance migrant and resident species were present in both landscapes and no difference in species richness was observed for these groups. The total abundance of long-distance migrants and interior species was higher in contiguous forest than expected, suggesting that the density of many of these species was higher in contiguous forest than in forest fragments. These results indicate that boreal forest birds suffer similar effects from habitat fragmentation caused by agriculture as do birds in other fragmented landscapes.

Bird communities in forest fragments in the boreal forest are not merely random samples from the species pool at the regional scale (Connor and McCoy 1979, Coleman et al. 1982, Møller 1987). Many species were more common in large fragments or in areas that were less isolated than would be expected if individuals were randomly distributed across the landscape (Freemark and Collins 1992, Hinsley et al. 1995). Species such as Tennessee Warbler, Magnolia Warbler, Black-throated Green Warbler, Bay-breasted Warbler, and Canada Warbler were all relatively common in contiguous forest, but were rare in the agricultural landscape. In particular, Tennessee Warbler was present at 81% of all contiguous forest sites but was present at only 26% of sites in the agricultural landscape. Clearly, non-random mechanisms influence the abundance and frequency of certain species between and within landscapes.

Many species in the boreal forest showed a preference for a specific forest type. In particular, white spruce and mixedwood stands supported very different bird communities than pure trembling aspen stands (Hobson and Bayne, in press). Aspen stands in the boreal forest of Saskatchewan usually have a relatively simple vertical structure, consisting of a dense 1–3 m shrub layer and the canopy. In contrast, white spruce and mixedwood stands are structurally more diverse, with greater plant diversity and structural heterogeneity at the shrub, subcanopy, and canopy levels (Hobson and Bayne, in press). As a consequence, mixedwood and white spruce stands have more nesting and foraging niches and tend to support more avian species than pure aspen stands. Regardless, differences among landscapes were usually similar among forest types indicating that the effects of forest fragmentation occur across a broad range of vegetation types.

In North America, lower densities of forest birds in forest fragments have typically been associated with processes related to differential reproductive success. Typically, nesting and pairing success are lower near edges and in small patches compared with forest interiors (Villard et al. 1993, Van Horne et al. 1995, Hagan et al. 1996). Although we did not have sufficient data to test for area effects on nest predation, our results suggest that predation and brood parasitism are higher in forest fragments than in contiguous forest. Whether increased nest predation is the cause of differences in avian community structure in the boreal forest is unclear. We have found that Ovenbirds in small forest fragments that were not successful at breeding are less likely to return to a site than successful breeders (Bayne 2000). In addition, Ovenbirds have much lower apparent annual survival in small forest fragments (34%) than in contiguous forest (62%, $P = 0.02$) which we attributed to increased dispersal from areas of high nest predation (Bayne 2000).

Andrén (1994) argued that landscape context may be a particularly important predictor of the severity of fragmentation effects. Our work supports this hypothesis; we found that area-sensitivity depended on the amount of forested land within 5 km. We found that a number of species associated with white spruce were area-sensitive, but only when fragments were isolated. Small patches that are close to other forest patches may be more suitable to forest birds than large isolated fragments for a variety of reasons. Resident species may be less likely to colonize isolated patches because of difficulties in dispersing across an open landscape (Matthysen and Currie 1996). For long-distance and short-distance migrants, nest predation may be more intense in isolated fragments than in small fragments in a landscape with higher local forest cover. Predation rates are often highly dependent on the amount of forested land in the landscape, probably because generalist predators typical of fragmented landscapes react more to landscape composition than to local fragment characteristics such as fragment size (Oehler and Litvatis 1996, Bayne and Hobson 1997, Donovan et al. 1997). Finally, birds may be able to move between patches in less isolated areas to obtain sufficient resources and may in fact defend territories in different patches (Rail et al. 1997).

In North America, most studies examining the effects of forest fragmentation on breeding bird assemblages have been conducted in landscapes that have been fragmented for long periods and that are considerable distances from large tracts of contiguous forest. We found little evidence that boreal forest birds considered area sensitive elsewhere are predisposed to coping with anthropogenic fragmentation any better than species occurring predominately in more southern forests. However, in boreal forest fragments surrounded by agriculture, American Redstart, Ovenbird, Hermit Thrush, and Connecticut Warbler were found in fragments considerably smaller than those 200 km south of our study area (Johns 1993). This suggests that birds may demonstrate a differential response to forest fragmentation, and particularly their choice of minimum fragment size, depending on distance from contiguous forest. However, Johns (1993) did not take into account the importance of random placement. The larger area requirements of long-distance migrants in the Aspen Parkland of Saskatchewan relative to the Boreal Forest may also be due to the fact that birds are regionally less abundant in the Aspen Parkland (Brown 1984).

Our recent examination of LANDSAT imagery for the southern boreal transition zone in Saskatchewan (i.e., that region of the Boreal Plains ecozone south of the commercial forest boundary) revealed that nearly 75% of this area has been cleared for agriculture since European settlement in the early 1900s. The consequences of the change from contiguous boreal forest to a landscape highly fragmented by agriculture have been the northern movement of avifauna associated with more open or parkland habitat, such as Clay-colored Sparrow, House Wren, American Goldfinch, and Brown-headed Cowbird. These species may benefit initially by the creation of a more open landscape containing boreal forest fragments. However, several species more typical of the Boreal Plains Ecozone, namely those resident and long-distance migrant species identified here, have lost a considerable portion of their habitat, and several of these species show some sensitivity to forest fragment size and isolation. These fragments may ultimately function as sink habitat for some species (Bayne 2000). Species of particular concern include Tennessee Warbler, Magnolia Warbler, Bay-breasted Warbler, and Black-throated Green Warbler. All of these species occurred less frequently than expected in the fragmented landscape. In addition, these species require mature to old mixedwood and white spruce forests that are currently under intense pressure from forestry companies, both in the agricultural and commercial forestry zones of the boreal forest.

We examined only the effects of fragmentation of boreal forest by agriculture, a process evident throughout the entire portion of privately owned or Crown leased lands in the Boreal Plains ecozone of Saskatchewan and largely typical of similar areas in Alberta and Manitoba. Fragmentation of the remaining boreal forest in these provinces of western Canada is also occurring through commercial forestry (Cumming et al. 1994, Stelfox 1995). Unlike fragmentation by agriculture, gaps created by forestry are usually temporary, and therefore may have less effect on avian communities in the long term (Schmiegelow et al. 1996, Drolet and Desrochers 1999). Harvested landscapes retain a forested matrix that may prevent the invasion of generalist predators that are adapted to human-dominated landscapes (Andrén 1995). Further studies are required to examine the long-term consequences of habitat loss and fragmentation on forest birds and other wildlife in both agricultural and commercial forest landscapes in western Canada. This will be particularly important as contiguous forests that might act as population sources for most boreal forest breeding birds become proportionately less available on the landscape.

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HABITAT AND LANDSCAPE CORRELATES OF PRESENCE, DENSITY, AND SPECIES RICHNESS OF BIRDS WINTERING IN FOREST FRAGMENTS IN OHIO

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ABSTRACT.—We investigated the distribution of wintering woodland bird species in 47 very small, isolated, woodland fragments (0.54–6.01 ha) within an agricultural landscape in north-central Ohio. Our objectives were to determine correlations between temporal, habitat, and landscape variables and avian presence, density, and species richness within the smallest woodlots occupied by such species. Our results suggest that even common species are sensitive to variation in habitat, landscape, and season. Woodlot area explained the most variation in presence, density, and species richness. Shrub cover was also an important predictor variable for presence of the smallest resident birds. Shrub cover might function as both a refuge from predators and as a windbreak, reducing thermal costs in a flat, open landscape. Landscape factors related to isolation and connectedness were also correlated with species presence and density. The species composition of the community changed through the winter, as did the density of individual species, suggesting that the winter season may play an important role in determining the distributions of bird populations across woodlots. The models presented here for Ohio birds in this specific landscape may have biological inference for other species in similar landscapes. *Received 16 August 1999, accepted 4 March 2000.*

The effects of habitat loss and fragmentation on avian species have received a great deal of attention. Both island biogeography theory (MacArthur and Wilson 1967) and metapopulation theory (Hanski and Gilpin 1997 for review) predict that species will be lost from habitat fragments because of higher extinction and lower colonization probabilities. The intervening landscape in mediating rates of metapopulation colonization (Wiens 1997).

The composition and long-term persistence of woodland bird communities depend on the habitat requirements and dispersal abilities of individual species. For example, the division of resident breeders into woodland interior and edge species produces different models of community structure (Bellamy et al. 1996). Furthermore, the presence or absence of a given avian species in a particular woodland fragment can result not only from the size and structure of the fragment itself, but also from the characteristics of the surrounding landscape (Merriam and Wegner 1992, Hinsley et al. 1995b).

Many researchers have assessed the effects of forest fragmentation on avian populations (Whitcomb et al. 1981, Blake and Karr 1987, Terborgh 1989, Villiard et al. 1995, Schmiegelow et al. 1997). Most of this work has focused on the breeding season and on Neotropical migrants, with fewer studies directed toward permanent resident species (Hinsley et al. 1995a, b; Bellamy et al. 1996; Nour 1997), especially during the non-breeding season (Blake 1987, Hamel et al. 1993, McIntyre 1995). Consideration of how variation among years affects the distribution of permanent resident birds has not often been addressed, and seasonal influences have received very little attention (McIntyre 1995, Nour 1997, Telleria and Santos 1997). In addition, few studies of woodland bird species diversity have included large numbers of small habitat patches (Opdam et al. 1984, Hinsley et al. 1995a, Bellamy et al. 1996, Nour 1997), where the most noticeable effects would be expected.

We surveyed woodland bird populations in an agricultural landscape in north-central Ohio, focusing on seasonal effects within very small habitat patches. We were particularly interested in the smallest patch size for the various permanent resident species, many of which had been found in previous studies to use all patch sizes surveyed (Robbins 1980, Humphreys and Kitchener 1982, Ambuel and Temple 1983, Freemark and Merriam 1986, Hamel et al. 1993). In Ohio, once continuous

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TABLE 1. Size distribution of 47 Ohio woodlots from 0.54 to 6.01 ha in which wintering birds were surveyed.

Size class (ha)	*n*
0–1	11
1–2	13
2–3	10
3–4	6
4–5	5
5–6	2

forest started to undergo fragmentation with the arrival of European settlers (early 1800s). Today, much of the remaining woodland in the northwestern half of the state exists as relatively small fragments within an agricultural matrix. Our study site in north-central Ohio is approximately 10% forested (Steiger et al. 1979).

The objective of our study was to determine how characteristics of the woods themselves, the surrounding landscape, and temporal or annual environmental variation are related to the presence, density, and number of wintering bird species.

METHODS

Study area.—We censused avian communities occupying 47 isolated woodlots in Crawford, Delaware, Marion and Morrow counties, Ohio, a 2602.79 km^2 landscape devoted principally to row-crop agriculture. The woodlots were dominated by either oak-hickory (*Quercus-Carya*) or beech-maple (*Fagus-Acer*) forest and ranged in size from 0.05 to 6.01 ha (Table 1). All were situated on flat terrain and isolated in that they were not connected to any other woodland by fencerow or ditch-side vegetative corridor. The minimum distance between any two of these woodlots was 0.5 km, so these woodlots were also isolated from each other. None of the woodlots in the study had bird feeders.

Bird censuses.—The woodlots were surveyed once during each of three survey periods during the nonbreeding seasons of 1993–1994 and 1994–1995. The three survey periods were early winter (28 October–23 December 1993; 5 November–15 December 1994), mid-winter (21 January–9 February 1994; 24 January–6 February 1995), and late winter (7–23 March 1994; 11–22 March 1995).

On each visit, our goal was to obtain a complete count of all birds within a woodlot. Each woodlot was searched systematically by walking a route designed to encounter all resident birds. A survey entailed first walking slowly once around the perimeter of the woodlot and then through the woodlot interior along north–south transects 50 m apart. Thus, we used a one-stage systematic sampling design in this study (Bart et al. 1998). All the woodlots were fringed by a 1–6 m wide zone of dense rose (*Rosa* spp.) and blackberry (*Rubus* spp.) shrub cover that would have hidden birds from interior transect counting. Therefore, during the perimeter walk, we counted all birds within this fringe. Because all censuses were conducted when there were no leaves on the trees or shrubs and because the woodlots were quite small, we assumed that our combination of perimeter and transect counting enabled us to detect every bird in residence, and that detection rates did not vary over the course of the winter.

Habitat and landscape variables.—For each woodlot we recorded 16 measures of size, structure, and degree of connectedness and isolation. We measured woodland area and amount of edge (perimeter) from ground-truthed 7.5-minute topographic maps. We also recorded woodlot type (oak-hickory or beech-maple), canopy height, and estimated to the nearest 5% the percentages of woodlot area covered by swamp, shrub, or herb/forbes.

We consider isolation to indicate how far apart different woodlots are from each other in the landscape, and connectedness to indicate how well such woodlots are connected by potential movement corridors. Extents of isolation and connectedness of each woodlot within the surrounding landscape were characterized from topographical maps as distance to the nearest wood, area of woodland within 0.5 km and 1.0 km, number of woodlots within 0.5 km and 1.0 km, distance to the nearest fencerow, and length of fencerow within 0.5 km and 1.0 km. Although measurements made at 0.5 km and 1.0 km scales were not independent, we were interested in the predictive power of landscape variables at these two scales.

Statistical analyses.—To alleviate problems caused by multicellinearity among independent variables and to obtain composite estimates of degrees of isolation and connectedness, we performed a principal component analysis using a correlation matrix of the eight landscape indices. If a small number of principal components explains a large amount of the variability in the data, and if biological interpretations can be attached to such components, such principal components represent "unmeasurable" factors (i.e., quantities that cannot be directly measured) that are responsible for generating the values of the variables actually measured (Bart and Notz 1994). Isolation and connectedness of habitat patches seem to be such unmeasurable concepts in the sense that there are so many possible ways to define and measure them.

To reduce the effect of pseudoreplication (Hurlburt 1984), for all statistical analyses, we randomly chose one of the six available censuses to represent each woodlot and stratified our woodlots by size so that all census time periods were represented equally across woodlot sizes. Thus, the sample size for all analyses was 47 woodlots. We chose this approach because it is the most conservative in terms of pseudoreplication and we did not want to average across all census pe-

TABLE 2. Landscape variable scores and proportion of variation in eight indices of isolation and connectedness of 47 woodlots explained by the first two principal components, PC1 and PC2. Eigenvalues are given in parentheses.

Landscape variable	Component PC1 (3.37)	 PC2 (2.05)
Distance to nearest woodlot	0.409	0.259
Number of woodlots within 0.5 km	−0.453	−0.209
Number of woodlots within 1.0 km	−0.429	−0.029
Area of woodland within 0.5 km	−0.379	−0.214
Area of woodland within 1.0 km	−0.377	−0.158
Distance to nearest fencerow	0.262	−0.467
Length of fencerow within 0.5 km	−0.205	0.557
Length of fencerow within 1.0 km	−0.218	0.538
Proportion of variance explained	0.421	0.256

riods because we were interested in the effects of year and season.

We employed logistic regression (Agresti 1990, Anonymous 1996) to examine the influence of woodland structure, surrounding landscape, and temporal variables on species presence. We used backward elimination based on P values for β estimates associated with each predictor. When discrete predictor variables had more than one level we coded them with dummy variables and checked the linearity of the logit (Hosmer and Lemenshow 1989). Variables with the least significance were dropped one-by-one from successive models.

We used multiple stepwise regression, with dummy-variables when appropriate (Neter et al. 1990, Anonymous 1996), to investigate the influence of habitat, landscape and temporal variables on individual species density and species richness. We checked for normality by examining residual plots (Neter et al. 1990) and arcsine-square-root transformed all proportions because they were not normally distributed. We also checked for multicollinearity following Weisberg (1985) and Neter and coworkers (1990). Most of the collinearity was resolved by our principal components analysis. However the variables area and edge were collinear ($r = 0.70$). We chose to leave both of these variables in the set of predictor variables rather than deleting one because of our biological interest in each. Only in Mourning Dove (*Zenaida macroura*), Red-Bellied Woodpecker (*Melanerpes carolinus*), and Hairy Woodpecker (*Picoides villosus*) did both of these variables occur in the final stepwise regression model. In these species we ran additional models with either area or edge, but not both as the predictor variable. We compared the parameter estimates and standard errors from these models because collinearity often results in unstable parameter estimates. In this respect, the parameter estimates were satisfactory and we left both area and edge in the final model.

Because of small sample sizes, analyses of presence, density, and species richness were not conducted for raptor species. We considered results with $P \leq 0.05$ to be significant for all analyses. We used Minitab (Anonymous 1996) on a Windows 98 platform to perform the above analyses.

The models presented here, although applicable statistically only to the woodlots we visited, should have explanatory power for landscapes similar to the one we studied.

RESULTS

Principal components analysis.—The first two principal components in our analysis (PC1 and PC2; Table 2) accounted for 68% of the total variation in the landscape-level variables and therefore provided a good summary of isolation and connectedness of the fragments. PC1 showed moderate to high negative loading for number of woodlots within 0.5 km and 1.0 km as well as for total area of woodland within 0.5 km and 1.0 km. PC1 had a high positive loading for distance to nearest woodlot. Therefore, we interpreted PC1 as an index of the amount and distance of woodland in the landscape surrounding each fragment, with higher scores of PC1 representing increased isolation.

PC2 showed high positive loading for the length of fencerow within 0.5 km and 1.0 km and high negative loading for distance to nearest fencerow (Table 2). We interpreted PC2 as indicating connectedness to other woodlands in the landscape, higher scores of PC2 representing increased connectedness. All principal components beyond PC1 and PC2 each explained less than 10% of the variation in landscape-level variables and so were omitted from further analysis.

Species presence.—(Detailed statistical tables are available from the authors upon request.) In the second year of the study, Tufted Titmice (*Baeolophus bicolor*) occupied fewer woodlots ($Z = -1.97$, 40 df, $P = 0.05$), while Downy Woodpeckers (*Picoides pubescens*) occupied more woodlots than the first year ($Z = 1.69$, 40 df, $P = 0.05$). As the winter season progressed, the probability of a woodlot being occupied by Tufted Titmice decreased from early to mid-winter ($Z = -1.92$, 40 df, $P = 0.05$) and increased from mid- to late winter ($Z = 2.65$ and 2.12, 40 and 43 df, respectively, $P < 0.05$ for both).

Presence of Carolina Chickadees (*Poecile carolinensis*) was positively associated with percent shrub cover ($Z = 1.90$, 44 df, $P = 0.05$), while Tufted Titmice were more likely to be found in oak-hickory than in beech-maple woodlots ($Z = 2.18$, 40 df, $P = 0.03$). Woodlot area was by far the most important predictor variable of presence, with 11 (61%) species showing a significant positive relationship with area (all with $P < 0.05$).

Presence of Downy Woodpeckers and Blue Jays (*Cyanocitta cristata*) was associated with an increase in edge ($Z = 2.85$ and 2.61, 44 and 45 df, $P < 0.01$ for both). Mourning Doves, Common Flickers, Red-bellied Woodpeckers, Northern Cardinals (*Cardinalis cardinalis*), Dark-eyed Juncos (*Junco hyemalis*), and Song Sparrows (*Melospiza melodia*) were less likely to be present as woodlots became more isolated (PC1; $Z = 2.93$, 1.86, 1.98, 2.30, 2.19, and 2.12; 45, 41, 43, 43, 45, and 43 df; $P < 0.05$ for all). Increasing connectedness of a woodlot (PC2) was associated with an increased probability of Common Flickers being present ($Z = 2.08$, 41 df, $P = 0.04$).

Densities in occupied woodlots.—(Detailed statistical results are available from the authors upon request.) Red-bellied Woodpeckers showed a decreased density in the second year of the study ($F_{131} = -2.86$, $P = 0.01$). Beta values for dummy variables coding for the three seasons showed densities of American Robins (*Turdus migratorius*) decreased from early to mid-winter. ($F_6 = 8.22$, $P = 0.02$). Densities of Mourning Doves and American Goldfinches (*Carduelis tristis*) increased from early to mid-winter and decreased from mid- to late winter ($F = 4.70$ and 53.73, 22 and 6 df, respectively, $P < 0.05$ for both). Woodlot area was significant in more models of avian density than any other variable with 11 (61%) of 18 species decreased in density with increased woodlot area (all $P < 0.05$). Densities of Red-bellied Woodpeckers, Downy Woodpeckers, and American Robins decreased as woodlot edge increased ($F = 4.68$, 14.72 and 15.22; 131, 35 and 6 df; respectively; all $P < 0.05$), while densities of Hairy Woodpeckers increased ($F_{24} = 5.14$, $P = 0.03$). Downy Woodpecker and Blue Jay densities increased with shrub cover ($F = 6.84$, 4.21; 35, 21 df; $P = 0.01$, 0.05, respectively) while American Robin density decreased ($F_6 = 10.45$, $P = 0.02$). Increased Tufted Titmouse density was weakly associated with increased herb/forb cover ($F_{24} = 3.12$, $P < 0.01$), while Hairy Woodpecker, Carolina Chickadee, and Northern Cardinal densities increased with increased swamp cover ($F = 93.37$, 4.30 and 7.84; 24, 15, and 18 df, respectively; $P < 0.05$ for all). Hairy Woodpeckers and Northern Cardinals were at higher densities in beech–maple fragments ($F = 9.60$ and 4.02, 24 and 18 df, respectively, $P < 0.05$ for both). Densities of Common Flickers, Red-bellied Woodpeckers, American Robins, and Northern Cardinals decreased with increased connectedness (PC2; $F = 10.17$, 8.18, 9.63, and 11.05; 68, 131, 6, and 18 df, respectively; $P < 0.05$ for all).

Species richness.—Species richness did not vary significantly between the two winters of the study. In the only statistically significant relationship, the number of species increased with woodlot area ($F_{45} = 27.36$, $P < 0.01$).

DISCUSSION

Certain properties of our sampling method may have biased our results (i.e., detectability may have differed among bird species, seasons, and woodlot sizes). Nevertheless, we consider our counts to be robust because the woodlots surveyed were small (<6 ha) and all surveys were conducted when there were no leaves. Since we performed many tests, some spurious significance is likely and our statistical inference may be weak. However our results seem reasonable and consistent with theory and other sources of information.

Temporal, woodlot, and landscape variables were significantly associated with variation in avian assemblages in island woodlots of north-central Ohio during winter. However, not all species responded in the same way to the variables we examined.

In comparing the two winters, we found differences in presence of woodpeckers and density of Red-bellied Woodpeckers. Annual variations in avian abundance have been shown in other studies (Telleria and Santos 1997, Bellamy et al. 1996) and are of considerable importance for calculating colonization and extinction rates, and resulting metapopulation dynamics (Verboom et al. 1991).

Presence and density of several permanent resident species decreased throughout at least part of the winter. Titmouse, chickadee, and Song Sparrow probability of being present decreased from early to mid-winter and increased from mid- to late winter. Although we did not find a relationship between species richness and year or season, others have detected significant relationships between avian species richness and season in small isolated woodlots, usually from comparisons between winter and breeding seasons (McIntyre 1995, Tellaria and Santos 1997).

One reason we may have detected changes in bird communities throughout the winter is because the Temperate Zone winter is a time of decreasing food abundance and high thermoregulatory cost, making it a stressful time of year, especially for resident birds. Mortality will probably progressively reduce numbers of birds over winter and this effect should result in fewer woodlots being occupied later during the season. Northern Ohio is near the northern edges of the ranges of Tufted Titmouse and Carolina Chickadee and so the effects of winter mortality on population measures might be stronger in these two species compared to other permanent resident species in our study. However, valid estimates of survivorship and the converse, mortality, can only be obtained from intensive mark-recapture studies. Mark-recapture studies will also provide some insight on whether birds are experiencing higher mortality rates in, or are emigrating more often from small woodlots.

The causes of winter mortality in forest fragments such as the ones we surveyed have not been studied. For example, we found a consistent trend for percent shrub cover in a woodlot to be positively associated with chickadee presence. Shrub cover may provide protection both from wind-induced convective heat loss and from hawk predation, allowing for greater winter survival. Such factors in combination with other within-woodlot effects and landscape attributes (e.g., isolation and connectiveness) may determine winter mortality and thus be of great importance to a comprehensive understanding of the demography of permanent resident birds in the Temperate Zone.

Species presence, density, and diversity were positively and most strongly associated with woodlot area. These area relationships have been seen in other studies (e.g., Hinsley et al. 1995b, Bellamy et al. 1996). Positive relationships with extent of woodlot edge were seen in some species, especially in edge and generalist species such as American Tree Sparrows, Blue Jays, and Downy Woodpeckers.

Increased isolation has long been predicted to result in fewer species (McArthur and Wilson 1967). We found increased woodlot isolation to be negatively associated with the presence of many species. In our study area, connectedness was associated with aggregate length of fencerow surrounding a woodlot. These fencerows may act not only as movement corridors but may be suitable habitat for some species. Our results suggest that the isolation and connectedness of a woodlot to the surrounding landscape play important roles in determining the occupancy and abundance of winter birds.

At the community level, we found that the richness of the avifauna increased significantly with patch area. While Blake (1987) and Tilghman (1987) also reported that species richness and diversity of wintering avifauna increased directly with forest tract size in eastern North America, Yahner (1985) reported no difference in abundance or diversity of wintering avifauna between fragmented and nonfragmented habitat in Pennsylvania. Yahner's study area was a 1166 ha managed forest that had been clear-cut in a rectilinear grid pattern so that "fragments" may not have been perceived as such by birds and certainly were not isolated from each other.

Hamel and coworkers (1993) found no effect of forest fragmentation on avian species richness or evenness during winter in a Tennessee agricultural landscape. While their study focused on isolated island woodlots, the smallest woodlot they examined was 17 ha and, judging from our results, may have been too large to cause any reduction of species diversity. By contrast, McIntyre (1995) censused woodlots as small as 3.25 ha during a Georgia winter and found woodlot size effects on bird species diversity.

Similar patterns have also been observed in Europe. In The Netherlands (Opdam et al. 1984, 1985; Van Dorp and Opdam 1987) and England (Hinsley et al. 1995a, Bellamy et al. 1996), the diversity of woodland birds has been monitored during the breeding season in landscapes very similar to ours. Despite the difference in seasons, their results closely resemble ours in depicting strong associations between species presence and both fragment area and isolation. Similarly, Haila (1981) in Finland and Tellaria and Santos (1997) in Spain found that the mean densities of individual wintering forest passerine species decreased with increasing forest size and that species diversity increased with patch size. Haila (1981) attributed this latter relationship to increased habitat diversity in larger patches.

The widespread occurrence of many common bird species may give the impression that their distributions are not particularly influenced by woodlot and landscape features. However, our results suggest that even common species are sensitive to variation in season, habitat, and landscape. Our models focused on Ohio birds in a specific landscape, but because the same approach can be used in many other landscapes, the biological inferences to be drawn from this study are extensive.

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BIRD ASSEMBLAGES OF PROTECTED AND EXPLOITED COASTAL WOODLANDS IN EAST-CENTRAL ARGENTINA

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ABSTRACT.—We surveyed vegetation and bird assemblages in protected and exploited woodlands in the warm temperate, coastal woodlands of Buenos Aires Province, Argentina. Exploited woodland experienced selective logging of *Celtis tala* until at least 1960; presently it is used for sheltering domestic livestock. Vertical structure and floristic composition were simpler in exploited than in protected woodland. Likewise, avian density and species richness were lower in exploited woodland. Viewing the avifaunas from a guild perspective, we found the insectivore guild and frugivore-insectivore guild differed substantially between protected and exploited woodlands. The bird densities of these guilds were higher in protected woodland, and the species richness of the insectivore guild was lower in the exploited woodland. Apparently the insectivore guild responded primarily to structural differences, whereas the frugivore-insectivore guild may have responded more to differences in floristic composition. The granivore guild also differed between the two woodlands, but primarily because of changes in the density of the Rufous-collared Sparrow (*Zonotrichia capensis*). This bird species was more abundant in the protected woodland. *Received 18 Oct. 1999, accepted 5 March 2000.*

Human modifications of forest structure have different influences on bird communities. Clear-cutting promotes a drastic reduction of density and species richness in bird assemblages inhabiting the forest interior and increases the abundance of birds associated with early successional stages and forest edges (Mannan and Meslow 1984, Probst et al. 1992, Annand and Thompson 1997). In contrast, selective logging has been suggested to have less effect on bird assemblages because this practice may produce smaller changes in vegetative structure (Hansen et al. 1995, Annand and Thompson 1997; but see Franzreb and Ohmart 1978). Domestic livestock also have a negative impact on birds inhabiting woodlands and forests, in part because they decrease understory herbaceous plant cover (Bock et al. 1993, Fleischner 1994). These patterns have been frequently reported for North American bird communities but, as Jaksic and Feinsinger (1991) suggested, North American temperate forests appear to be quite different than their South American counterparts. At the same time, there are few studies on the effects of natural or human habitat alterations on avian assemblages in southern South America (but see, Marone 1990, Willson et al. 1994, Lopez de Casenave et al. 1998, Aleixo 1999).

Coastal woodlands in Buenos Aires Province (east-central Argentina) have suffered considerable degradation because of human activities. Since the end of the eighteenth century, travellers have commented on the exploitation of these woodlands [see Concolocorvo 1773 (1942)]. The main human activities have been the extraction of firewood and charcoal (Cabrera 1949). The woodlands also have been used to shelter domestic livestock (Parodi 1940) or have been eliminated for mining (Parodi 1940). Biogeographical and distributional patterns of the birds of Buenos Aires Province are well known (Narosky and Di Giacomo 1993, Cueto and Lopez de Casenave 1999). The ecology of birds inhabiting the coastal woodlands, however, has been little investigated (but see Cueto 1996).

Here, we report on bird assemblages and vegetation structure in old-growth and second-growth coastal woodlands; the latter are known to have been selectively logged until about 1960 and presently are used for sheltering domestic livestock. We evaluated the following questions: (1) Are there differences between the old-growth and second-growth woodlands in terms of vegetation structure and floristic composition? (2) Are there differences in total bird density and species richness between old-growth and second-growth woodlands? (3) Are there differences in bird

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density within trophic guilds between old-growth and second-growth woodlands?

METHODS

Study area.—We conducted the study at the Private Reserve "El Destino" (35° 08′ S, 57° 25′ W, 2400 ha) on the coast of de la Plata River, Buenos Aires Province, Argentina. This reserve is part of the Biosphere Reserve "Parque Costero del Sur" (26,581 ha; CEPA 1989). Tala-coronillo woodlands occupy 11.4% (ca 274 ha) of the Reserve "El Destino" (Cagnoni et al. 1996). Dominant species of the canopy stratum are *Scutia buxifolia, Celtis tala, Schinus longifolius, Jodina rhombifolia, Sambucus australis,* and *Ligustrum lucidum.* Common species of the shrub stratum are *Pavonia malvacea* and *Sida rhombifolia.* Some vines (*Clematis denticulata, Passiflora coerulea,* and *Parthenocissus quinquefolia*) and an epiphyte (*Tillandsia aeranthos*) grow on the trees and shrubs. The herbaceous stratum is dense and continuous, principally consisting of *Oplismenopsis najada, Parietaria debilis,* and *Euphorbia portulacoides* (Cagnoni et al. 1996).

The climate is wet, warm temperate, with hot summers and mild winters. Frosts are infrequent because of proximity to the river. The mean annual precipitation is 885 mm (n = 10 years); the rainiest months are January and February (summer). The mean maximum temperature is 27.5° C and the mean minimum temperature is 5.9° C.

We studied an old-growth tala-coronillo woodland, which has been free of direct human disturbance at least since the beginning of this century (hereafter protected woodland). It is among the few surviving coastal woodlands where the original physiognomy was not altered by forestry practices (Goya et al. 1992). The other woodland was selectively logged for *C. tala* until about 1960 (hereafter exploited woodland). Trees recovered from exploitation mainly by stump sprouting. Today, the exploited woodlands provide shelter for domestic livestock, and the presence of animals appears to reduce the density and extent of the understory. We could not choose our woodlands in a way that controlled for this variable; therefore, any patterns in our data undoubtedly reflect the composite effects of past selective logging and present understory alteration.

Vegetation measurements.—We randomly located eight plots (30 × 30 m) in both protected and exploited woodlands during December 1992 and March 1993. In the center of the plot we established a 15 m transect in each of the four cardinal directions. We sampled vegetation structure at 30 random points on each transect by erecting a rod marked at 1 m intervals at each point and recording the height and species identity of vegetation contacting the rod. The horizontal cover of each tree species was calculated as the percentage of points where the species was present. We averaged values over the four transects for each plot. We depicted profiles of foliage cover as the percentage of points with contacts at 1 m intervals.

Bird surveys.—We sampled bird populations in December 1993 (spring), March 1994 (summer), June 1994 (autumn), and September 1994 (winter) using fixed-radius point counts (Verner 1985, Hutto et al. 1986). Morrison and coworkers (1981) recommended the use of four to six points to obtain a stable estimation of bird density in homogeneous areas (i.e., a single physiognomic class of vegetation dominates the site) such as those in coastal woodlands (Ribichich and Protomastro 1998). Therefore we sampled the bird populations in six randomly located points in each type of woodland. All points were separated from each other at least 150 m. We sampled each point four times for 4 hr or less, beginning 30 min after sunrise, and again during the last 3 hr of daylight. At each point two persons recorded the number of birds seen or heard within 25 m from the center. Using two observers decreased the likelihood of missing birds that were present and improved confidence in species identifications. Sampling began immediately upon arrival at the count area and was continued for 10 min. Birds that flushed from within 25 m upon the observers' arrival were recorded as present (Hutto et al. 1986). We took special precaution to avoid counting the same individual more than once because this is the most important assumption of the method (Verner 1985).

Bird densities were averaged for each sample point over the four counts. We used the bird densities of the 12 spatial replicates (6 in each type of woodland) to avoid temporal pseudoreplication. Species richness per point on each sampling occasion was expressed as the cumulative number of species recorded in the four counts.

Bird species were assigned to three trophic guilds; insectivores, frugivores-insectivores, and granivores based on published data of feeding habits (Short 1975, Canevari et al. 1991, Davis 1993, Montaldo 1993) and observations of foraging behaviors (Cueto 1996; Cueto and Lopez de Casenave, unpubl. data).

Statistical analysis.—We evaluated differences in horizontal plant cover and vegetation profiles between the protected and exploited woodlands with the two-tailed t-test or the Mann-Whitney U-test when the assumption of normality was violated (D'Agostino-Pearson K^2 test; Zar 1996).

We evaluated differences in bird density, species richness, and guild density between the protected and exploited coastal woodlands by using Two Factor Analysis of Variance with Repeated Measures on One Factor (Winer 1971) because we counted birds in the same points at every season. We used the Tukey multiple comparison test for comparing means and the simple effect test when the interaction between season and woodland was significant (Winer 1971). We tested equality and symmetry of covariance matrices (Winer 1971). Data for frugivore-insectivore guild violated the symmetry assumption, so in this case we used the Greenhouse-Geiser procedure (Lower Bound Epsilon correction, $\epsilon = 0.333$) to adjust the degrees of freedom of within-subject effects (Winer 1971). All statistical analyses were implemented using SPSS/PC+ 4.0 (No-

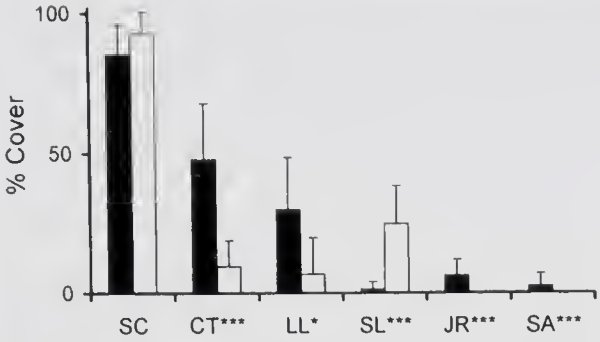

FIG. 1. Mean horizontal coverage (1 SD indicated by vertical line) of tree species in the protected (solid bars) and exploited woodland (open bars) at the Reserve "El Destino", east-central Argentina. Asterisks indicate significant differences between woodlands (two-tailed *t*-test or Mann-Whitney *U*-test; $n = 8$; * $P < 0.05$; *** $P < 0.001$). Tree-species acronyms, SC: *Scutia buxifolia*, CT: *Celtis tala*, LL: *Ligustrum lucidum*, SL: *Schinus longifolius*, JR: *Jodina rhombifolia*, and SA: *Sambucus australis*.

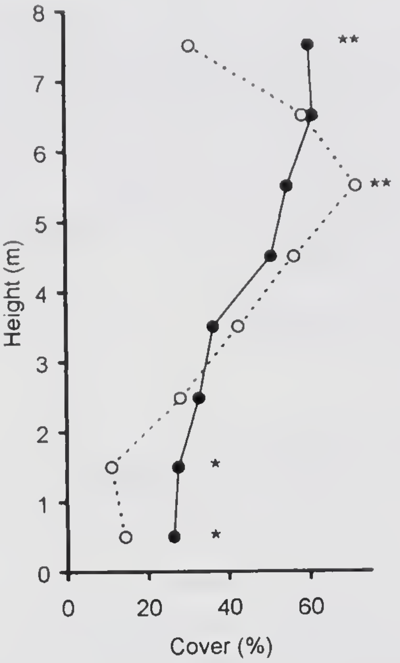

FIG. 2. Mean profiles of foliage cover in the protected (●) and exploited woodland (○) at the Reserve "El Destino", east-central Argentina. Asterisks indicate significant differences between woodlands (two-tailed *t*-test: $n = 8$; * $P < 0.05$; ** $P < 0.01$).

rusis 1986) for DOS. We used a $P < 0.05$ as our level of accepted significance.

RESULTS

Vegetative structure of woodlands.—The tree species with greatest horizontal cover in the two woodlands was *S. buxifolia,* which did not show differences between the woodlands (Fig. 1). Other species showed important differences in cover between woodlands: *C. tala, L. lucidum, J. rhombifolia,* and *S. australis* had significantly smaller horizontal coverage in the exploited woodland, while *S. longifolia* showed the reverse pattern (Fig. 1).

The vertical distribution of vegetation cover in the protected woodland was relatively uniform between ground and 4 m, then increased slowly, reaching the greatest foliage cover over 7 m (Fig. 2). The undercanopy stratum was principally composed of low trees (e.g., *J. rhombifolia* and *S. australis*) and *L. lucidum* saplings, and the canopy by *S. buxifolia* and *C. tala.* The exploited woodland had less plant cover at low strata (Fig. 2) because undercanopy species present in the protected woodland were missing and there were few *L. Lucidum* saplings. Above 3 m foliage cover increased, peaking at 5–6 m, and then declined rapidly (Fig. 2). The most important species in the canopy of the exploited woodland was *S. buxifolia,* followed by *S. longifolia* and *C. tala.*

Bird assemblages.—Total density of birds in the protected woodland was higher than in the exploited woodland at every season (Table 1, Fig. 3A). In addition, total density showed seasonal changes in both woodlands (Table 1). Seasonal changes were due to differences between spring and autumn densities (Tukey test: $P < 0.01$), principally in the protected woodland (Fig. 3A).

Similar patterns were found in terms of species richness. At every season, bird species richness had greater values in the protected than in the exploited woodland (Table 1, Fig. 3B). Bird species richness varied seasonally in both woodlands (Table 1). Seasonal variations in species richness were due to lower values in autumn (Tukey test: $P < 0.05$), mainly in the protected woodland (Fig. 3b).

Insectivorous bird density in the protected woodland was higher than in the exploited woodland at every season (Table 2, Fig. 4A). The density of this guild did not show seasonal changes in either woodland (Table 2). During spring and summer, we recorded 10 species in the protected woodland, whereas in the exploited only 4 species were found. In autumn and winter the number of species in this guild was similar in both woodlands (Table 3). Tropical Parula (*Parula pitiayumi*), House Wren (*Troglodytes aedon*), Rufous-browed Peppershrike (*Cyclarhis gujanensis*), and Masked Gnatcatcher (*Polioptila dumico-*

TABLE 1. Summary of Two Factor Analysis of Variance with Repeated Measures on One Factor for the total bird density and species richness in the protected and exploited coastal woodlands at the Reserve "El Destino," east-central Argentina. (MS = Mean squared).

		Total bird density			Species richness		
Source of variation	df	MS	*F*	*P*	MS	*F*	*P*
Between woodlands							
Woodland	1	1913.2	33.5	0.0002	58.5	46.1	0.0001
Point count (woodland)	10	57.1			1.3		
Within woodlands							
Season	3	352.2	3.9	0.02	11.5	3.3	0.04
Season × woodland	3	108.6	1.2	0.3	2.0	0.6	0.6
Season × point count (woodland)	30	91.1			3.5		

la) were the most abundant species of the guild; all of them showed higher densities in the protected woodland (Table 3).

The frugivore-insectivore guild had a higher density in the protected woodland than in the exploited woodland (Table 2) during spring and summer (Fig. 4B). Frugivore-insectivore guild density showed seasonal changes in both woodland types (Table 2). Seasonal changes were the result of higher densities in spring and summer (Tukey test: $P < 0.001$; Fig. 4B). The number of species of this guild was similar in both woodlands and its seasonal changes may be attributed to the arrival of migratory species, such as Small-billed Elaenia (*Elaenia parvirostris*) and Streaked Flycatcher (*Myiodynastes maculatus*) during spring and summer (Table 3). Frugivore-insectivore guild differences between woodlands in spring were due to the greater abundance of Small-billed Elaenia in the protected woodland, whereas in summer they were due to the higher abundance of Creamy-bellied Thrush (*Turdus amaurochalinus*), Rufous-bellied Thrush (*Turdus rufiventris*), Great Kiskadee (*Pitangus sulphuratus*), and Small-billed Elaenia in the protected woodland (Table 3).

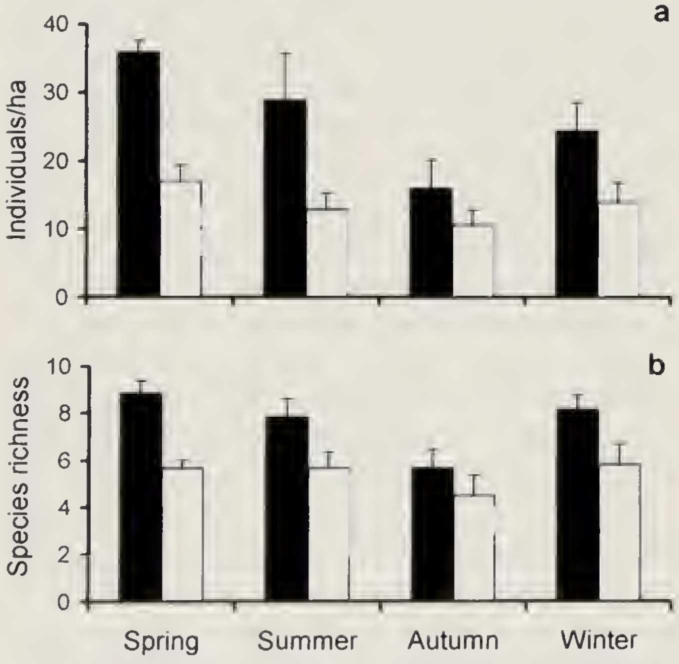

FIG. 3. Mean seasonal variation (1 SE indicated by the vertical line) of the (a) total density of birds and (b) species richness in the protected (solid bars) and exploited woodland (open bars) at the Reserve "El Destino", east-central Argentina.

The density of the granivore guild showed an interaction between woodlands and seasons (Table 2). Bird abundance was higher in the protected woodland only in spring and winter (Simple effect test; spring: $F_{1,30} = 8.35$, $P < 0.01$; winter, $F_{1,30} = 6.66$, $P < 0.05$; Fig. 4C). Seasonal changes and differences between woodlands largely reflect variation in the density of Rufous-collared Sparrow (*Zonotrichia capensis*; Table 3).

DISCUSSION

We found important effects on bird density and richness, as well as on the densities of the three trophic guilds between protected and exploited woodlands. As our study was carried out in only two woodlands and we could not perform an experimental manipulation, our results did not show directly that logging and domestic livestock have been the cause of such differences. However, based on the woodlands' history and our observations in the surrounding areas, we believe that the differences in avian assemblages are most likely

TABLE 2. Summary of Two Factor Analysis of Variance with Repeated Measures on One Factor for the insectivore, frugivore-insectivore, and granivore guilds in the protected and exploited coastal woodlands at the Reserve "El Destino", east-central Argentina. Probabilities for within woodland effects of the frugivore-insectivore guild have been adjusted with the Lower Bound Epsilon correction ($\epsilon = 0.333$). (MS = Mean squared).

		Insectivore			Frugivore-insectivore			Granivore		
Source of variations	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Between woodlands										
Woodland	1	494.1	32.0	0.001	160.5	5.5	0.04	81.0	9.0	0.01
Point count (woodland)	10	15.4			29.4			9.0		
Within woodlands										
Season	3	41.7	2.1	0.1	276.0	16.2	0.02	89.8	7.1	0.001
Season × woodland	3	7.5	0.4	0.8	60.8	3.6	0.09	40.0	3.2	0.04
Season × point count (woodland)	30	20.2			17.1			12.7		

related to the woodlands' histories rather than to idiosyncratic or confounding factors.

Unlike some other forests where selective logging appears to affect bird assemblage only weakly (Hansen et al. 1995, Annand and Thompson 1997), we found a strong reduction in both total bird density and species richness in the exploited woodland. This result could be related to the natural regrowth of the trees. *Celtis tala* has a pronounced capacity for resprouting (Hunziker and Dottori 1976) that appears to be the principal mechanism of tree regeneration, judging by the virtual absence of seedlings and saplings (Ribichich and Protomastro 1998). Resprouting promotes a structure of thin branches and a low canopy. Furthermore, present use of the exploited woodlands by domestic livestock could be responsible for the reduction in cover of some tree species (e.g., *J. rhombifolia, S. australis,* and *L. lucidum*). There is evidence that reduced vertical structure and decreased floristic diversity have a negative impact on bird assemblages (Holmes and Robinson 1981, Rice et al. 1983, Rotenberry 1985).

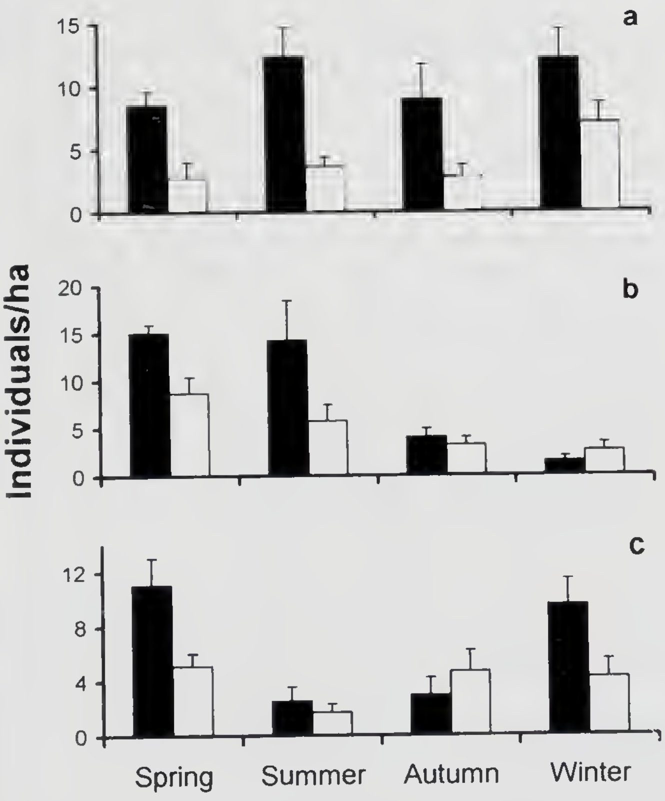

FIG. 4. Mean seasonal changes (1 SE indicated by vertical line) of (a) the density of insectivore, (b) frugivore-insectivore, and (c) granivore guilds in the protected woodland (solid bars) and exploited woodland (open bars) at the Reserve "El Destino", east-central Argentina.

We found that the abundance and species richness of insectivorous birds were higher in the protected woodland. The bird species of this guild search for food mainly in foliage by gleaning and hovering at different heights (Cueto 1996). In the exploited woodland foliage was dense between 5 and 6 m, but reduced (relative to the protected woodland) at low strata as well as in the top of the canopy. Sparser foliage correlates with lower density and richness of insectivorous birds in other temperate forests (Maurer and Whitmore 1981, Franzreb 1983; but see Darveau et al. 1992).

The density of frugivorous-insectivorous birds varied among seasons in both woodlands, but during spring and summer was higher in the protected than in the exploited woodland. Cueto and Lopez de Casenave (un-

TABLE 3. Trophic guild assignments and density of bird species (individuals/ha) in protected (PW) and exploited (EW) woodlands at "El Destino" Reserve, east-central Argentina. Bird names after Meyer de Schauensee (1970). Guild abbreviations: FI, frugivores-insectivores; G, granivores; I, insectivores.

Species	Spring		Summer		Autumn		Winter	
	PW	EW	PW	EW	PW	EW	PW	EW
Picazuro Pigeon, *Columba picazuro* (G)	1.27	0.43	0.43	1.49	0.85	3.18	1.27	1.70
Eared-dove, *Zenaida auriculata* (G)	—	0.42	0.21	0.21	—	—	—	—
White-tipped Dove, *Leptotila verreauxi* (G)	1.06	0.43	0.21	—	—	0.64	1.27	0.42
Narrow-billed Woodcreeper, *Lepidocolaptes angustirostris* (I)	0.85	—	0.21	—	—	—	0.85	—
Tufted Tit-spinetail, *Leptasthenura platensis* (I)	0.21	—	—	—	0.21	—	0.42	0.21
Sooty-fronted Spinetail, *Synallaxis frontalis* (I)	0.64	—	0.43	—	—	—	—	—
Chicli Spinetail, *Synallaxis spixi* (I)	—	—	0.64	—	0.42	—	2.33	—
Pale-breasted Spinetail, *Synallaxis albescens* (I)	—	—	0.21	—	—	—	—	—
Freckle-breasted Thornbird, *Phacellodomus striaticollis* (I)	0.21	—	—	—	—	—	—	—
Blue-billed Black-tyrant, *Knipolegus cyanirostris* (I)	0.21	0.21	—	—	—	—	—	0.21
Streaked Flycatcher, *Myiodynastes maculatus* (FI)	0.42	—	—	0.21	—	—	—	—
Great Kiskadee, *Pitangus sulphuratus* (FI)	0.64	1.70	2.12	1.91	0.43	1.06	0.42	0.85
White-crested Tyrannulet, *Serpophaga subcristata* (I)	0.43	—	0.64	0.42	—	0.21	0.64	0.64
Small-billed Elaenia, *Elaenia parvirostris* (FI)	12.01	3.40	1.91	0.64	—	—	—	—
House Wren, *Troglodytes aedon* (I)	0.85	0.21	3.18	0.42	0.85	1.06	3.40	0.64
Masked Gnatcatcher, *Polioptila dumicola* (I)	0.64	—	1.06	—	2.55	0.42	—	2.12
Rufous-bellied Thrush, *Turdus rufiventris* (FI)	1.06	2.34	5.09	2.34	2.97	2.12	1.06	1.70
Creamy-bellied Thrush, *Turdus amaurochalinus* (FI)	0.85	1.27	5.10	0.64	0.64	—	—	—
Rufous-browed Peppershrike, *Cyclarhis gujanensis* (I)	1.27	0.43	0.21	0.21	2.33	—	1.06	0.21
Tropical Parula, *Parula pitiayumi* (I)	3.18	1.91	5.52	2.55	2.12	0.85	3.18	2.55
Golden-crowned Warbler, *Basileuterus culicivorus* (I)	—	—	0.21	—	0.42	0.21	0.21	0.21
Rufous-collared Sparrow, *Zonotrichia capensis* (G)	8.91	3.82	1.70	—	2.12	0.85	7.00	2.12

publ. data) found that seasonal changes in density of this guild were associated with the fruiting patterns of tree species, principally *C. tala, L. lucidum, J. rhombifolia,* and *S. australis.* Differences in density of the frugivorous-insectivorous birds between woodlands during spring and summer (the fruiting seasons; Murriello et al. 1993) could thus be related to differences in the coverage of those plant species that were more abundant in the protected woodland (Fig. 1). Outside the fruiting period (autumn and winter; Murriello et al. 1993), the density of this guild did not differ substantially between woodland types, suggesting that floristic composition was more important than vegetation structure in the habitat used by the frugivorous-insectivorus birds. Other researchers suggest that habitat selection by frugivorous birds correlated closely with fruit availability (e.g., Martin and Karr 1986, Levey 1988, Loiselle and Blake 1993, Rey 1995).

Spatiotemporal variations in the granivore guild as a whole resulted primarily from patterns in one abundant species, Rufous-collared Sparrow. Cueto and Lopez de Casenave (unpubl. data) suggest that seasonal variation in Rufous-collared Sparrow densities reflects the higher food abundance during winter and the greater availability of nesting sites during spring in the coastal woodlands. Our data on Rufous-collared Sparrow in the protected and exploited woodlands support this hypothesis. This species frequently nests on the ground under shrubs, and consumes seeds and litter invertebrates on the ground (Canevari et al. 1991). The exploited woodland provided less cover in the lower strata than the protected woodland; the herbaceous cover was sparse as well. We infer that as a result Rufous-collared Sparrows encountered fewer nesting and foraging opportunities in exploited than in protected woodland. Why the density of this species decreased during summer and autumn in both woodlands was not clear.

Our results indicate that old-growth woodland alterations promoted by past logging and present sheltering of livestock brought about reductions in the abundance and richness of bird assemblages. At present logging effects on birds could be more severe than those reported in this study. New studies are needed to identify the similarities and differences between recently and old logged woodlands and the impact on bird assemblages to determine if our results apply to other Chacoan forests.

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A COMPARISON OF 1983 AND 1994 BIRD SURVEYS OF POHNPEI, FEDERATED STATES OF MICRONESIA

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ABSTRACT.—Relative abundance and habitat use of 29 forest bird species, including 22 land birds (18 indigenous breeding residents, 3 exotics, 1 migrant) along with a rail, heron, and five seabirds (shearwater, tropicbird, 3 terns) were assessed on Pohnpei [Island] during summer 1994 and compared with the results of the first survey in 1983. The most frequently encountered species in both surveys were the Purple-capped Fruit-Dove (*Ptilinopus porphyraceus*), Pohnpei Lory (*Trichoglossus rubiginosus*), Micronesian Starling (*Aplonis opaca*), and Micronesian Honeyeater (*Myzomela rubratra*). Among the five species endemic to Pohnpei, the Pohnpei Mountain Starling (*Aplonis pelzelni*) verges on extinction, with only one confirmed sighting in nearly 50 years; the Long-billed White-eye (*Rukia longirostra*) is vulnerable to encroaching agriculture in its preferred and limited montane habitat, where nearly 90% of the sightings were on approximately 10% of the land area, and the Pohnpei Lory (*Trichoglossus rubiginosus*), Pohnpei Flycatcher (*Myiagra pluto*), and Pohnpei Fantail (*Rhipidura kubaryi*) are widespread and common, but were less frequently encountered in 1994 than in 1983. The total number of birds encountered per observation station during 8-minute point counts in each of six elevation zones was 67–80% fewer in 1994 than in 1983. Encounter rates (birds/hour) were reduced by at least 50% in both uplands and lowlands in at least 14 of 29 species; none of the 29 showed an overall increase. Artifacts of sampling and sampling bias may have contributed to reduced observation rates, but anecdotal evidence suggests a decline in numbers is real and may be attributed to combined effects of habitat degradation, hunting practices, and possibly predation by introduced species. Protection of the upland forests from further degradation and more frequent monitoring to better assess population trends are recommended. *Received 26 Oct. 1999, accepted 15 April 2000.*

The first quantitative surveys of Micronesian birds were conducted in the early 1980s by the U.S. Fish and Wildlife Service (USFWS); Pohnpei was surveyed during May and June 1983 (Engbring et al. 1990). The most recent (and first follow-up) survey was supported by the South Pacific Regional Environment Programme (SPREP) through the South Pacific Biodiversity Conservation Programme and the South Pacific Regional Avifauna Conservation Programme. The survey was conducted in May and June 1994 and its results are reported here. The 1983 and 1994 surveys were confined to forest habitats, the most widespread vegetation type on the island and the principal or sole habitat type for all the single island endemics and otherwise rare species. Habitat preferences and relative abundance were assessed for the same 29 species in both years, and the 1994 team attempted to duplicate as close as possible the routes and methods of the original survey.

STUDY AREA AND METHODS

Study area.—Pohnpei is a roughly circular 23 km diameter five million year old volcanic dome (355 km^2 in area) located 766 km north of the equator in the Eastern Caroline Islands, Federated States of Micronesia (Fig. 1; MacLean et al. 1986, Merlin et al. 1992, Office of Budget, Planning and Statistics 1994). Maximum recorded elevation is 772 m at Nahnalaud (U.S. Geological Survey 1983) with at least ten other peaks in the central highlands exceeding 600 m (U.S. Army Corps of Engineers 1986). Densely forested, steep ridges and deep valleys radiate outward and downward to foothills and coastal lowlands, including a mangrove zone up to about 2 km wide. A discontinuous barrier reef encloses a lagoon up to 6 km wide along with numerous volcanic and coral reef islets. The major vegetation types are native upland forest, agroforest (where fruit trees and other agricultural plants are grown among forest trees, preserving much of the original canopy and understory), mangrove forest, secondary vegetation, and swamp forest. Grasslands, marshes, croplands, urban areas, barren regions, and aquatic areas are minor components, together contributing about 6% of the total area (MacLean et al. 1986).

Warm, humid conditions prevail throughout the year. The average annual temperature is 27° C and the average monthly temperature does not vary from the annual average by more than 1° C (Laird 1982). Relative humidity averages 80–90%. Mean annual rainfall in Kolonia is approximately 485 cm, with no month averaging less than 25 cm (U.S. Army Corps of Engineers 1986), with as much as 1,051 cm/yr estimated

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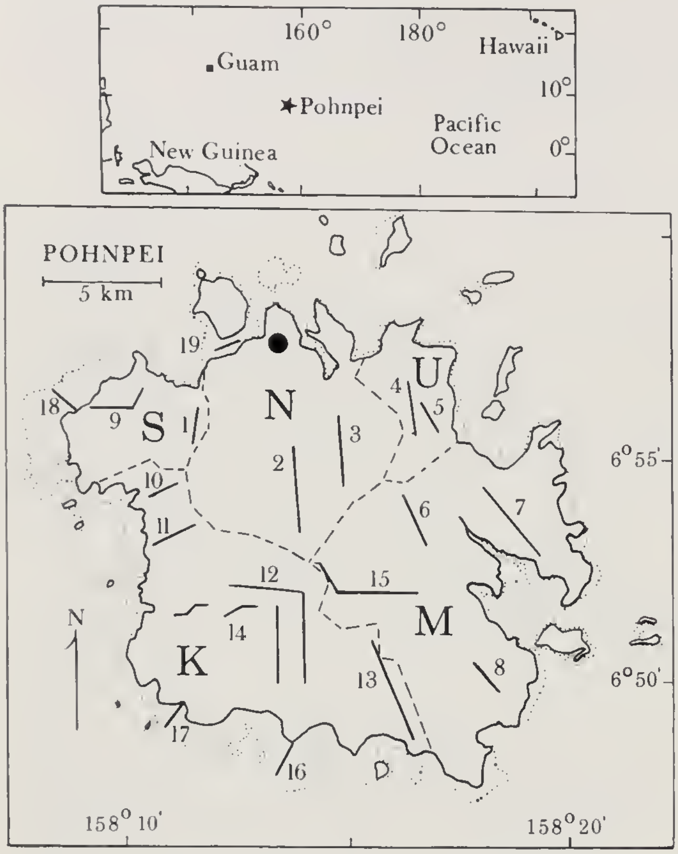

FIG. 1. Location of Pohnpei and transects for summer 1994 forest bird survey; municipality abbreviations are K = Kitti, M = Madolenihmw, N = Nett, S = Sokehs, U = U; ● = Kolonia.

for the mountains (Merlin et al. 1992). The 1983 survey was conducted during the most severe drought in Pohnpei history, with precipitation through May totaling only 24 cm (Engbring et al. 1990). The 1994 survey was conducted under more normal weather conditions with 177 cm of precipitation recorded during January–May, closely approximating the mean (183 cm) for the years 1961–1990 (Kolonia Weather Station records; H. Simon, pers. comm.).

Subsistence farming is widespread in the vicinity of the settlements; the chief crops are banana (*Musa*), breadfruit (*Artocarpus*), coconut (*Cocos*), yam (*Dioscorea*), taro (*Alocasia, Colocasia,* and *Cyrtosperma*), tapioca (*Manihot*), and sakau (*Piper methysticum*; U.S. Army Corps of Engineers 1986).

Habitat and elevation zones.—Habitat and vegetation type correlate broadly with elevation on Pohnpei; I followed Engbring and coworkers (1990) in calculating bird species distribution separately in six elevation zones (Table 1), which I merged into uplands (> 200 m) versus lowlands (< 200 m) for comparisons between species and survey years (Table 2).

Mangrove forest, dissected by natural streams and manmade channels, forms a nearly continuous belt around the island covering about 55 km² (Petteys et al. 1986). It reaches its greatest width (2 km) along the southern and western shores. Clearcutting, landfills, dredging, and other commercial and private developments continue to encroach on this habitat, especially in the vicinity of settlements. Mature forest is dominated by *Rhizophora, Bruguiera, Sonneratia,* and *Xylocarpus*. The understory is open and the canopy is about 20–30 m high.

The 0–100 m zone includes populated coastal lowlands, river valleys, agroforest, and patchy native forest along with marshes, grassy areas, and dense thickets of *Hibiscus*.

The 100–200 m zone is similar to the lower zone but the slopes are steeper, the native forest is more extensive, and agroforest and human habitation less pervasive. Common forest plants include the hardwoods dohng (*Campnosperma brevipetiolata*), seir en wai (*Cananga odorata*), sadak (*Elaeocarpus carolinensis*), karara (*Myristica insularis*), and ais (*Parinari laurina*) along with tree ferns (katar; *Cyathea* spp); the ivory nut palm (oahs; *Metroxylon amicarum*) is common in the wetter areas. The canopy is about 25–35 m high.

The 200–400 m zone is largely unpopulated. Steep hillsides are covered in native broadleaf forest with a canopy about 25–35 m high. Madeau (*Cinnamomum carolinense*) is locally common and kotop (*Clinostigma ponapensis*), an endemic palm, becomes more numerous near the upper limits of the zone. Tree ferns and young palms dominate the understory.

The 400–600 m zone grades imperceptibly from the

TABLE 1. Characteristics for 1983[a] and 1994 Pohnpei forest bird survey stations.

		Number of stations		Birds per station[c]		
Elevation (m)	% of area[b]	1983	1994	1983	1994	% difference
Sea level[d]	15.7	44 (9.6%[e])	36 (11.9%)	38.6	12.6	−67.4
0–100	40.7	130 (28.4%)	56 (18.5%)	71.0	15.9	−77.6
100–200	17.5	78 (17.0%)	79 (26.1%)	67.9	16.2	−75.4
200–400	15.8	92 (20.1%)	77 (25.4%)	63.3	16.4	−74.2
400–600	8.4	89 (19.4%)	48 (15.8%)	57.5	13.9	−75.8
600–800	1.9	25 (5.5%)	7 (2.3%)	44.4	9.0	−79.8

[a] Based on data from Engbring et al. 1990.
[b] Percent of the total area for all elevation zones combined; calculated from data in Engbring et al. (1990).
[c] Calculated as the mean number of observations of the 18 species of indigenous land birds, pigeons through passerines.
[d] Mangrove forest.
[e] Percentage of the total number of stations.

lower one but has steeper slopes and more extensive areas of palm forest. Depending on edaphic conditions, the upper limits abut, gradually merge with, or form a narrow transition zone into cloud forest.

The cloud forest predominates on steep slopes, razorback ridges, and mountain summits at 600–800 m in elevation. The trees (many of the species also occurring at lower elevations) are only 5–10 m tall and are festooned with mosses, liverworts, and ferns, which also carpet the forest floor. Shrubs are common, including the high elevation endemic melastome, duduhmwoal (*Astronidium ponapense*). Patches of the high elevation endemic pandanus (*Pandanus patina*) occur in the flatter and wetter areas. Kotop palms are present, but not on the highest crests.

Survey methods.—Three survey teams, each consisting of a primary counter (team leader), usually two secondary counters (mainly College of Micronesia students), and one or two local guides recorded all birds seen and heard over unlimited distance during single eight-minute sessions at each of 303 stations (observation points) distributed 200 m apart along 19 forest transects islandwide, 23 May–3 June 1994 (Fig. 1, Table 1). Transects were selected using topographic maps (U.S. Geological Survey 1983) to provide widespread coverage of the island in roughly the same pattern as the 1983 survey. The specific routes were determined by local topography, and the distances between points were measured with topometric hipchains. The straight lines in Fig. 1 are an abstraction because the rugged terrain made it impossible to follow compass bearings very far. Roads and settled areas were excluded from both surveys.

Several practice sessions preceded the actual survey to familiarize the visiting biologists with the local avifauna and to introduce survey techniques to participants unfamiliar with them. The counts began at sunrise and none was initiated after 11:00. They were suspended whenever adverse weather conditions made detection difficult. At the end of each eight-minute session, the counters compared and pooled their results. The team leaders included C. Faanes and C. Rowland (U.S. Fish and Wildlife Service, mainland and Honolulu offices, respectively) and the author. To compare our results with those of the previous surveys, I calculated the encounter rates (birds per station and birds per hour by elevation zone) for each species and applied a χ^2 goodness of fit test for significance.

I followed Engbring and coworkers (1990) in excluding migrants (and vagrants) with the exception of the Long-tailed Cuckoo (*Eudynamis taitensis*). I included seabirds that nest and roost in the forested parts of the island along with several primarily grassland or savanna species and the Rock Dove (*Columba livia*), which occurs widely among the villages and settlements but is unestablished in native forest habitats. Vernacular and scientific names are from Pratt and coworkers (1987).

RESULTS

Rare species.—Six of the 29 species were recorded only once during all point counts in 1983 and 1994 combined. The Pohnpei Mountain Starling (*Aplonis pelzelni*), endemic to Pohnpei, is almost certainly the rarest resident bird species on the island, with only one confirmed [specimen] record (postdating both surveys) during the past 50 years (Buden 1996). Local residents claim to see it in the mountains from time to time, but I have encountered none in the past seven years other than the specimen obtained in July 1995.

The introduced Rock Dove (*Columba livia*) and the Long-tailed Cuckoo (*Eudynamis taitensis*), an austral winter visitor to Micronesia from New Zealand, likewise were unrecorded during both surveys. Small flocks of 5–10 domesticated pigeons were observed in Kolonia in 1983 and 1994. More recently, local residents informed me of other flocks in outlying settlements virtually around the entire island in all five municipalities. However, *C. livia* seemingly remains unestablished in and tends to avoid native forest habitats. The Long-tailed Cuckoo was observed one time each by the 1983 and 1994 teams, but not on point counts. I have not encountered it on Pohnpei proper, but recorded it on visits to outlying atolls, including Mokil (Buden 1995) and Kapingamarangi (Buden 1998), and the residents of Sapwuahfik Atoll consider it a regular visitor to their islands (Buden 1999).

Audubon's Shearwater was counted once and observed on five other occasions by the 1983 team. None was counted in 1994, but I heard several calling in the Lehn Mesi valley southwest of Nahnalaud, about midway to the village of Salapwuk at 05:00 on 26 May 1994. Audubon's Shearwater roosts and breeds in burrows in the more remote parts of the island (Engbring et al. 1990), and because it is vocal only at night the methodology undercounts it. Its status is difficult to assess but it probably continues to breed in small numbers in the central highlands. The most recent records are several I heard calling from a wooded hillside overlooking the harbor just north of Kolonia at dawn several times in May 2000.

The White-browed Crake (*Porzana cinerea*) and Short-eared Owl (*Asio flammeus*) were encountered only once each in 1994 and not at all in 1983. A crake was heard calling in mangroves (transect 18, station 13) at about 08:45 on 24 May and an owl was seen in lowland marsh (transect 7, station 10) at about 08:

TABLE 2. Encounter rates (individuals per hour) of forest birds in upland and lowland habitats on Pohnpei during summer surveys in 1983[a] and 1994.

Species and status[b]	Above 200 m		Below 200 m		% difference[c]	
	1983	1994	1983	1994	Uplands	Lowlands
Audubon's Shearwater (R) (*Puffinus lherminieri*)	?	0	?	0	NC	NC
White-tailed Tropicbird (R) (*Phaethon lepturus*)	4.6	1.3	2.6	1.4	−72***	−46
Pacific Reef-Heron (R) (*Egretta sacra*)	?	0	?	0.3	NC	NC
Red Junglefowl [chicken] (I) (*Gallus gallus*)	9.4	1.7	21.8	2.0	−82***	−91***
White-browed Crake (R) (*Porzana cinerea*)	0	0	0	0.1	NC	NC
Brown Noddy (R) (*Anous stolidus*)	35.9	4.1	43.4	6.2	−89***	−86***
Black Noddy (R) (*Anous minutus*)	0	0	0.7	0.3	NC	−57
White Tern (R) (*Gygis alba*)	2.9	1.4	6.3	2.1	−52*	−67**
Rock Dove (I) (*Columba livia*)	0	0	0	0	NC	NC
Caroline Islands Ground-Dove (R) (*Gallicolumba kubaryi*)	0	0.2	0.6	0.2	NC	−67
Purple-capped Fruit-Dove (R) (*Ptilinopus porphyraceus*)	105.5	16.9	109.8	16.0	−84***	−85***
Micronesian Pigeon (R) (*Ducula oceanica*)	4.4	1.0	1.3	0.5	−77***	−62
Pohnpei Lory (R*) (*Trichoglossus rubiginosus*)	63.2	16.6	52.9	13.4	−74***	−75***
Long-tailed Cuckoo (NBV) (*Eudynamis taitensis*)	0	0	0	0	NC	NC
Short-eared Owl (R) (*Asio flammeus*)	0	0	0	0	NC	NC
Island Swiftlet (R) (*Aerodramus vanikorensis*)	5.5	4.1	6.2	4.7	−26	−24
Micronesian Kingfisher (R) (*Halcyon cinnamomina*)	13.3	6.2	21.0	5.6	−53***	−73***
Cicadabird (R) (*Coracina tenuirostris*)	0.3	0.1	0.7	0.4	−44	−75
Pohnpei Flycatcher (R*) (*Myiagra pluto*)	22.7	7.4	27.2	7.0	−67***	−74***
Pohnpei Fantail (R*) (*Rhipidura kubaryi*)	12.6	4.7	23.3	4.9	−63***	−79***
Caroline Islands Reed-Warbler (R) (*Acrocephalus syrinx*)	2.6	1.4	5.9	2.5	−49	−58***
Pohnpei Mountain Starling (R*) (*Aplonis pelzelni*)	0	0	0	0	NC	NC
Micronesian Starling (R) (*Aplonis opaca*)	58.0	20.6	64.6	19.1	−64***	−71
Micronesian Honeyeater (R) (*Myzomela rubratra*)	82.7	21.7	96.2	30.5	−74***	−68***
Caroline Islands White-eye (R) (*Zosterops semperi*)	6.1	0.9	10.0	1.2	−85***	−88***
Gray White-eye (R) (*Zosterops cinereus*)	37.6	7.2	60.9	10.4	−81***	−83***
Long-billed White-eye (R*) (*Rukia longirostra*)	25.0	4.1	2.6	0.5	−84***	−83***

TABLE 2. CONTINUED

Species and status[b]	Above 200 m 1983	Above 200 m 1994	Below 200 m 1983	Below 200 m 1994	% difference[c] Uplands	% difference[c] Lowlands
Blue-faced Parrotfinch (R) (*Erythrura trichroa*)	0	0	0.6	0.4	NC	−33
Hunstein's Mannikin (I) (*Lonchura hunsteini*)	0.2	0.2	3.5	1.4	NC	−60

[a] Data from Engbring et al. (1990).

[b] R = indigenous breeding resident, NBV = nonbreeding visitor, I = introduced and established, * = endemic to Pohnpei.

[c] Percent increase (+) or decrease (−) in encounter rate (1983 to 1994), with results of χ^2 goodness of fit test for rates standardized to 10 hours (1983 vs 1994); 1 df, *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$, NC: no comparisons, insufficient data.

30 on 23 May. The skulking habits of the crake and its predilection for densely vegetated wetlands doubtless have contributed to the paucity of sightings; its current status on Pohnpei is uncertain but it probably remains an uncommon resident in low wetlands. In Micronesia, the Short-eared Owl is resident only on Pohnpei; the endemic subspecies (*A. f. ponapensis*) is dubiously distinct from the nominate form (Engbring et al. 1990). Population estimates of the owl on Pohnpei have been low for several decades, ranging upwards to as many as about 50 birds during the mid-1950s (Marshall 1962). Reports from local Pohnpeians, including responses to questionnaires I distributed regarding recent sightings, suggest it is more numerous than the literature indicates. Most of the reports I received were of day-time sightings usually in open grassy or weedy areas, or at the forest edge. Bruce Crossan (pers. comm.), former Peace Corps Director for Pohnpei reported four seen together in a savanna area just outside of Kolonia about 18:00 on 30 March 1997.

Uncommon species.—I include Huntstein's Mannikin (*Lonchura hunsteini*) as "uncommon" despite 123 observed in 1983 (111 in the 0–100 m zone) and 32 in 1994. The introduced mannikin is common in grassy, weedy areas in the lowlands but absent from true forest. The indigenous Blue-faced Parrotfinch (*Erythrura trichroa*), also primarily a grassland or savanna species, probably has always been uncommon on Pohnpei, even in its preferred habitat (Engbring et al. 1990). Harvey Segal (pers. comm.), a naturalist residing on Pohnpei for 31 years, recalled seeing parrotfinches in the past but none in recent years. I have seen no more than five or six in the past seven years. The Pacific Reef-Heron (*Egretta sacra*) is seen regularly in coastal areas, but only occasionally in the interior, mainly along rivers, and the Black Noddy (*Anous minutus*) also is more numerous in coastal habitats. The Caroline Islands Ground-Dove (*Gallicolumba kubaryi*; 0.04 birds/station in 1983 and 0.02 in 1994) and the Cicadabird (*Coracina tenuirostris*; 0.06 birds/station in 1983 and 0.02 in 1994) were among the least frequently encountered species during both surveys; their populations have always been low, at least in historical times (Engbring et al. 1990, Baker 1951).

Common species.—Three species of seabirds roost and breed regularly in the forests of Pohnpei. The Brown Noddy (*Anous stolidus*) was the most numerous in both surveys, averaging 43.4 encounters per hour in the lowlands in 1983 but 1994 encounter rates were 89% and 86% lower in uplands and lowlands, respectively. The White-tailed Tropicbird (*Phaethon lepturus*) and White Tern (*Gygis alba*) also were frequently seen in the forest but less often in 1994 than in 1983 (Table 2).

Fourteen land birds among the 29 forest bird species are sufficiently abundant as to be encountered on average at least once during several hours in the field in suitable habitat. All 14 showed a reduction in encounter rate between 1983 and 1994 except the Caroline Islands Ground-Dove, which was unrecorded above 200 m in 1983 but observed twice in 1994.

In 1994, in decreasing order of abundance, and in uplands as well as lowlands, the four most abundant species were the Micronesian Honeyeater (*Myzomela rubratra*), Micronesian Starling (*Aplonis opaca*), Purple-capped

Fruit-Dove (*Ptilinopus porphyraceus*), and Pohnpei Lory (*Trichoglossus rubiginosus*). The same four were also the most numerous in the uplands in 1983, but in a different order (fruit-dove, honeyeater, lory, starling), whereas in the lowlands, the Gray White-eye (*Zosterops cinereus*) displaced the lory from the list for the fourth position and the starling was ranked third.

DISCUSSION

There have been no known additions, extinctions, or extirpations to the resident avifauna between 1983 and 1994, but encounter rates declined markedly for nearly all species in all forest habitats. The reduction in total birds per observation station for 18 native resident land birds ranges from 67.4–79.8% in each of six major elevation zones (Table 1). Among the 17 of 29 forest species with encounter rates of at least 0.5 birds/hr in 1983 and 1994, 15 (88%) had encounter rates reduced by at least 50% (Table 2); none increased.

To what extent this reduction reflects actual widespread decline in populations is uncertain. The 1983 survey was during a severe El Niño induced drought. The ordinarily lush and verdant landscape was more sere and sparse and may have enhanced detectability. Birds may have been more active in search of diminished resources caused in part by widespread fires. The possibility of a bias between survey teams with respect to their interpretation of multiple calls and sightings at a single station as belonging to one bird or to more than one also exists. However, multiple observers working in concert during both surveys (at least 2–3 overall in 1983 and 2–3 per team in 1994) would tend to moderate any single observer bias. These and other possible artifacts of sampling notwithstanding, my overall impression is of relatively few birds in the forest island-wide. Two surveys 11 years apart do not establish a trend by themselves. But if population numbers are reduced as much as anecdotal evidence would seem to indicate, several factors can be hypothesized as contributing to that decline.

Predation mainly by introduced species may account for some losses among birds. Rats (*Rattus* spp.) are the most common potential avian predators on the island. The black or roof rat (*R. rattus*) is the most numerous rat and occurs from sea level to high mountain ridges, whereas the Polynesian rat (*R. exulans*) occurs mainly in grasslands and lower montane forest, and the Norway rat (*R. norvigicus*) is found only locally in some areas of human habitation (Jackson and Strecker 1962). Although the detrimental effects of rats on many island populations of birds is well documented (e.g., Garnett 1984, Seitre and Seitre 1992, Milberg and Tyrberg 1993), Strecker and Jackson (1962) reported that rats on Pohnpei fed largely on plants and invertebrates. There is no evidence to suggest that rat populations are more numerous in forest habitats now than in the past or that birds have become a more important part of their diet.

Domestic cats (*Felis catus*) are common house pets in the settlements, and I have often seen spoor of feral cats throughout the central highlands where they are extremely secretive. They doubtless prey on birds, but Marshall (1962) reported that rats were their primary prey. Wild pigs (*Sus scrofa*) are scarce, if still extant, as is the monitor lizard (*Varanus indicus*), which was introduced during the early 1900s (Buden 2000). The Short-eared Owl is the only bird of prey on the island but it feeds mainly on rats and only occasionally on birds (Marshall 1962). It probably has always been present in small numbers (Engbring et al. 1990). The possible role of parasitic infections or introduced avian diseases in reducing bird numbers on Pohnpei has not been investigated.

Excessive hunting may have depleted populations of certain game species, especially the Micronesian Pigeon. Baker (1951:195), quoting from Coultas' field notes of 1930 stated that "two or three years ago, 4–5 Japanese [professional hunters], each, averaged from 75–100 birds [Micronesian Pigeons] per day," and Baker (1951:195) went on to say that even as early as the 1930s, Coultas considered it a "rapidly disappearing species on Pohnpei." Resident Pohnpeians still hunt birds and children often target them with slingshots or pellet guns. The Micronesian Starling is the most frequently eaten songbird. I find it difficult to reconcile the exceedingly small number of hunters encountered in the forest with the drastically reduced numbers indicated by the 1994 survey for virtually all species. Journeys of several days across the island are often completed without encountering anyone else in the forest, and the sounds of gunshots, which would be expected to carry long distances in the valleys are very seldom heard. On the other hand, the failure of the Micronesian Pigeon to rebound in the years following prohibition of professional hunting also is puzzling.

If the decline in bird numbers is real, one possible contributing factor is the progressive loss or alteration of habitat. Trustrum (1996), basing his conclusions on aerial photo analyses, reported a decline in native upland forest from 42% of the total vegetation cover in 1975 to 15% in 1995, which he attributed largely to cultivation of sakau (= kava in Fiji; *Piper methysticum*). Although the interior of Pohnpei is densely vegetated, the clearcutting of 1–2 ha plots for the cultivation of sakau has increased in recent years, reaching to the edge of the cloud forest at about 600 m in some areas. W. Raynor (Director of The Nature Conservancy on Pohnpei) has achieved some measure of success in encouraging traditional leaders to adopt a program to have local farmers "plant low," but resistance is high because sakau grows best on the wet mountain slopes and patches in such remote areas are perhaps less likely to be pilfered.

At least two of the five species of birds endemic to Pohnpei are nearly confined to high elevation forest and are the most seriously threatened by encroaching agriculture. The cloud forest is probably the last bastion for the Pohnpei Mountain Starling (Buden 1996), which formerly occurred also at lower elevations (Baker 1951). The Long-billed White-eye is nearly as confined with 89% of the observations in 1983 and 88% of those in 1994 being from elevations above 400 m, which comprise only about 10% of the total land area (Table 1). The uplands are also the primary habitat of the Micronesian Pigeon.

The disparity in numbers of birds observed between the two surveys merits further investigation. Protection of the upland forests from further degredation and more frequent monitoring of bird populations to better assess population trends is strongly urged.

ACKNOWLEDGMENTS

I am grateful to the South Pacific Regional Environment Programme (SPREP) for supporting this project and appreciate the assistance provided by the U.S. Fish and Wildlife Service, the Pohnpei State Government, and the Federated States of Micronesia National Government. F. Curren, former Secretary of Micronesia Islands Conservation (MIC) drafted the original proposal and coordinated travel and housing accommodations for all visiting off-island personnel. B. Raynor (The Nature Conservancy, Pohnpei) and V. Santiago (Pohnpei Division of Forestry) arranged for local guides to be selected via traditional municipality leaders. The designated guide leaders were W. Dickoi (Madolenihmw), J. Joakim (Kitti), E. Ladore (U), B. Padahk (Nett), and A. Zared (Sokehs). The other participating guides were B. Altis, D. Ardus, C. Augustine, V. Cantero, K. Clarence, P. David, P. Eperiam, D. Jack, J. Joakim, D. Jona, K. Kosmas, M. Padahk, J. Silbanuz, A. Tipen, R. Waltu, C. Washington, and E. William. R. Smith, U.S. Fish and Wildlife Service, Pacific Islands Office, generously provided a rental vehicle and arranged coverage of field expenses for part of the survey team. H. Anson (Pohnpei Division of Forestry) furnished transport for selected overland transects and arranged for use of the forestry boat piloted by T. Tom for surveys of the mangroves. F. Mendiola and D. Morgan, Pohnpei Utilities Corporation, allowed us access to lands surrounding the Kolonia water supply. A. Lorens, Pohnpei Division of Agriculture let us use Ag Station property for practice sessions and the late R. Etscheit allowed access to his private lands for additional practice. I especially appreciate the contribution of College of Micronesia student assistants whose knowledge of local birds proved a definite asset during field counts and who were able to serve as interpreters for the team leaders and their nonEnglish-speaking guides. The student participants were M. Miguel, J. Santiago, R. Nakasone, T. Sehpin, R. Silbanuz, and S. Tachepliyang.

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Short Communications

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Forehead Feathers of the Pied-Billed and Atitlán Grebes

Robert W. Storer[1,3] and Martin J. Muller[2]

ABSTRACT.—In grebes of the genus *Podilymbus*, the upper barbs of the forehead feathers are fused with the shaft into a somewhat flattened, pointed structure. We believe that when raised, these feathers may indicate a low probability of attack. *Received 8 Nov. 1999, accepted 18 March 2000.*

The Pied-billed Grebe (*Podilymbus podiceps*) and the extinct Atitlán or Giant Pied-billed Grebe (*P. gigas*) are unique among grebes in having the outer barbs of their forehead feathers fused with the end of the shaft into a stiff, somewhat flattened, pointed structure (Fig. 1). Examination of study skins has shown that these feathers first appear as the growth of the primaries of the juvenal plumage nears completion and are found in all subsequent plumages and in all species and subspecies of the genus. When these feathers lie flat against the head, most appear as shiny black with a small whitish tip and a thin line down the feather, giving the crown a finely spotted appearance. R.W.S. has checked museum specimens of all the species of grebes and has not found such feathers in any other grebe species nor have we seen a description of such feathers in print. Our objectives in this paper are to determine in which plumages they are found, the behaviors associated with raised feathers, and to speculate on their possible function.

For several reasons, we do not think that the structure or function of these feathers is related to the white down of the plumage that they replace. The white on the forehead of the small young is variable in extent and may be absent or nearly so. As the young grow, the pattern is lost on the top of the head but remains on the sides of the head. As the pattern on the crown is lost, the feathers that replace it are a blackish brown similar to the hue of the new forehead feathers; in all subsequent plumages these feathers are the same color; therefore, we doubt that individual recognition is a function.

The presence of these feathers in all plumages suggests that their function is not limited to the breeding season but used throughout the year. At times, these feathers are somewhat raised, giving a bristly appearance to the forehead, while at other times, they lie flat against the head (Fig. 2).

Grooming is a possible function, although an unlikely one. From field observations, M.J.M. found that during an oiling session, the birds obtain oil by squeezing the uropygeal gland between the tips of the mandibles. Given that only rapid, glancing contact is made between the forehead feathers and the oil gland, and when swabbing the back with the head during bathing contact is made largely or entirely with the crown and nape, any grooming function by these feathers seems unlikely.

We also believe that sun bathing is not involved. The skin beneath the forehead feathers of the Pied-billed Grebe is not pigmented; the feathers lack the pattern of black and white in those found over the areas where heat from the sun is absorbed (Storer et al. 1976), and the raising of these feathers is independent of whether or not the sun is shining.

A tactile use is another possibility, but we know of no behavior in which one bird touches another with these feathers.

We propose that these feathers might have a signal function. In his analysis of various behavior patterns photographed at Green Lake, Seattle, Washington, M.J.M. found the feathers raised in specific contexts (Table 1). When the feathers are raised, the birds are unlikely to attack unless provoked. Considering

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FIG. 1. Forehead feather of the Pied-billed Grebe. Length of part shown 4.5 mm. Drawing by John Megahan.

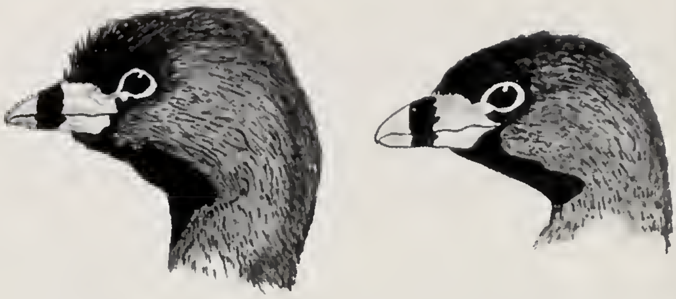

FIG. 2. Left, head of a female Pied-billed Grebe with the forehead feathers raised. Right, that of a male with the forehead feathers lowered. Drawings by Martin J. Muller.

that Pied-billed Grebes are very aggressive and are armed with a stout bill powered by a heavy musculature (Zusi and Storer 1969), there might well be a selective advantage in using signals that would reduce the likelihood of attacks. This might be especially advantageous in Pied-billed Grebes, which spend much time in areas of emergent vegetation where visual distances are short and unseen birds may suddenly approach from nearby. It should also be noted that grebes often attack from under water, and diving, which is always preceded by a slicking down of all feathers including those of the head, usually eliciting a fleeing response from another bird (except its mate and dependent young), especially when the dive is made towards that bird.

Why do the feathers have a stiff shaft? We believe that the advantage of such feathers is that they can be more effectively and more reliably raised and lowered when the feathers are wet. Because we have observed no instance in which these feathers are in contact with another bird, we think that the pointed end may be merely an artifact of the fusion of the outer barbs with the rhachis, which is probably the simplest developmental way to produce the thickening.

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TABLE 1. Behavioral contexts[a] in which head feathers of Pied-billed Grebes were raised.

Resting	pork-pie attitude
Self maintenance	swimming shake, upright bathing, oiling, head rubbing
Alarm	alert posture
Agonistic behavior	Circle Display (by wing-quivering male)
	Bluff Diving (male on surface raises feathers as other male dives, lowering them as other male resurfaces)
Sexual behavior	Advertising
	Triumph Ceremony (by male as members of pair approach each other)
	post-copulatory Water Trampling (as active bird turns to face passive bird)

[a] The terminology is that of Muller and Storer (1999). The patterns capitalized are considered ritualized displays or ceremonies.

Wilson Bull., 112(3), 2000, pp. 413–415

Evidence of an Increasing Hooded Merganser Population in Massachusetts

H W Heusmann,[1,3] T. J. Early,[1] and B. J. Nikula[2]

ABSTRACT.—The number of Hooded Merganser (*Lophodytes cucullatus*) broods hatching in nest houses on 53 study areas in Massachusetts increased by 289% from 1979–1983 to 1994–1998 and the number of areas used increased from 9 of 53 in 1979 to 26 of 53 by 1998. The number of Hooded Mergansers counted on 21 Massachusetts Christmas Bird Count circles from 1979–1983 to 1994–1998 increased by 225%. The increasing trend lines did not match, suggesting different populations. This appears to support reports of increasing Hooded Merganser populations by other northeastern state waterfowl biologists. *Received 16 Nov. 1999, accepted 12 April 2000.*

The Hooded Merganser (*Lophodytes cucullatus*) is the least common of the 3 species of mergansers occurring in North America (Bellrose 1976). Information on population trends is meager. Because they nest in forested areas at low densities (Dugger et al. 1994), they are minor species not tracked on new waterfowl breeding surveys in eastern Canada (Wilkins and Cooch 1999) or the northeastern states (Heusmann and Sauer 2000). The annual Midwinter Waterfowl Survey does not separate mergansers by species (J. Serie and A. Vecchio, unpubl. data). Biologists in Maine (R. B. Allen, unpubl. data), New Hampshire (E. G. Robinson, pers. comm.), Vermont (W. J. Crenshaw, unpubl. data), and New York (B. L. Swift, pers. comm.) however, report that Hooded Mergansers appear to be increasing. We documented an increase in Hooded Mergansers in Massachusetts by examining the 20 year history of merganser use in Wood Duck (*Aix sponsa*) nest houses and tallies of Christmas Bird Counts over the same period.

Between 1979 and 1998, Wood Duck nest houses located on 53 sites throughout Massachusetts (Fig. 1) were checked in July or August at the end of the nesting season. Heavily used sites were checked more frequently so we could more accurately detect second use of a house. Additional nest houses were installed on individual sites as Wood Duck use increased, so there was always a surplus of houses.

Use of houses was determined by the presence of at least 1 or more Wood Duck or Hooded Merganser egg or egg remains. A successful nest was one in which at least 1 duckling hatched. Occasionally, mixed species clutches were encountered. For this study, each clutch was assigned to one species or the other based on the identification of the incubating hen, the preponderance of eggs, or by shell fragments (Soulliere 1987).

We also tallied data from the annual Christmas Bird Count (CBC; Bock and Root 1981). Because the number of CBC count circles in Massachusetts has increased over the past 2 decades, our analysis was restricted to 21 circles located throughout Massachusetts with a history of counts between 1979 and 1998. To minimize annual variations, we compared 5 year averaged counts at the beginning and end of the 20 year period. Increased observer participation within circles can increase counts (Bystrak 1971). However, changes in observer participation in circles for which no or few mergansers were counted had little influence on the count. Therefore, we compared the average number of party hours for 7 circles that contained at least two-thirds of the Hooded Mergansers counted, for 1979–1983 and 1993–1997 (party hours for 1998 were not available).

The number of Hooded Mergansers hatched

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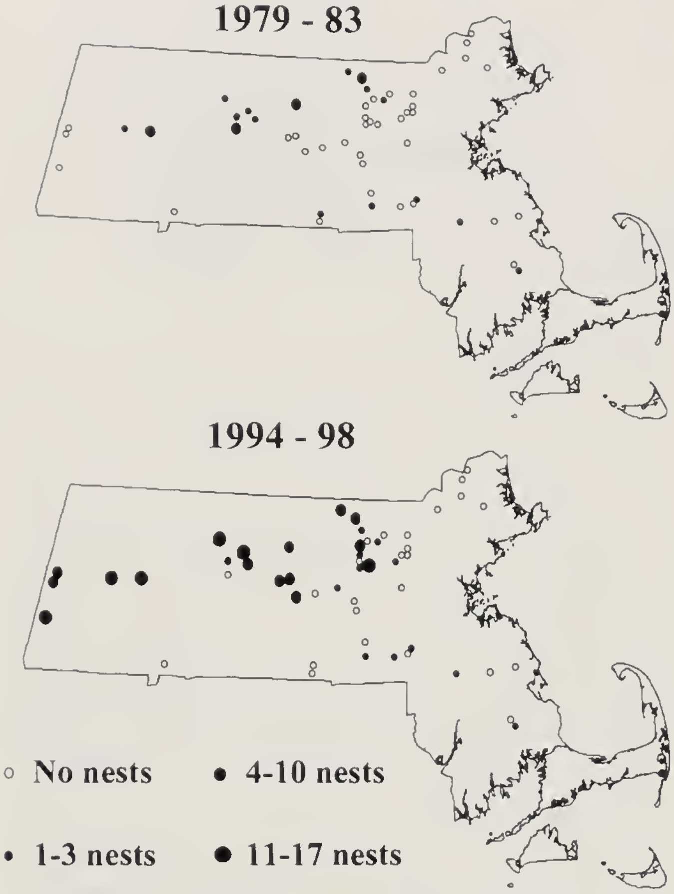

FIG. 1. Wood Duck nest house study sites in Massachusetts and changes in Hooded Merganser use, 1979–1983 versus 1994–1998.

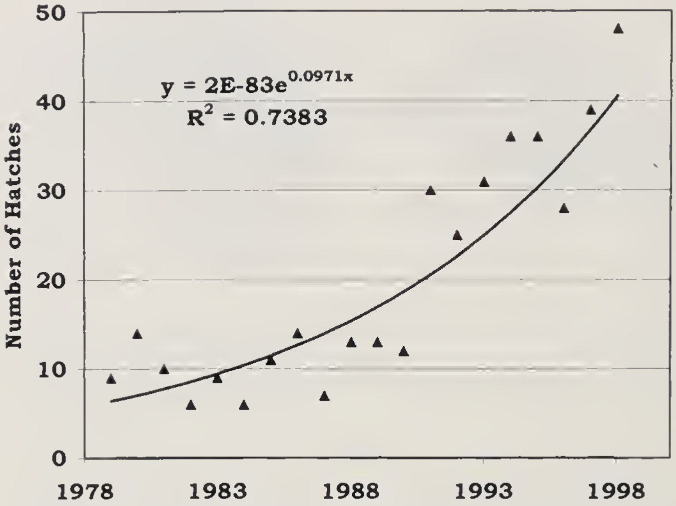

FIG. 2. Hooded Merganser hatches in nest houses on 53 Massachusetts study sites, 1979–1998.

in our study area nest houses increased over the 20 year period (Fig. 2), averaging 9.6 (range 6–14, mean SE 1.15) hatches during 1979–1983 and 37.4 (range 28–48, mean SE 2.88) during 1994–1998, a 289% increase. This was double the rate of increase for Wood Ducks hatched from the same study areas (from 143.4 to 328.8; Heusmann and Early, unpubl. data). The areas used by Hooded Mergansers for nesting increased from 9 of 53 sites in 1979 to 26 of 53 sites by 1998.

Twenty years of CBC data suggest an increasing population trend as well (Fig. 3). The total number of Hooded Mergansers counted on the 21 circles increased from an average of 350 [± 26.89 (SE), range 294–463] during 1979–1983 to 1139 (± 128.97, range 864–1690) during 1994–1998, a 225% increase. There was little evidence to suggest this increase was related to an increase in observer participation. During 1979–1983, the ratio of party hours to Hooded Mergansers counted was 1:0.44 in the 7 circles where two-thirds or more of the mergansers were observed. During 1993–1997, the ratio was 1:1.14. The number of party hours spent in a circle are likely less important for counting waterfowl occurring in flocks on open water than for more secretive passerine species (Raynor 1975).

Both nesting data and winter counts indicate that Hooded Mergansers have increased in Massachusetts over the past 2 decades (Figs. 2, 3). The pattern of the increase, however, has not been identical. Christmas Bird Counts were stable until 1984 when an increasing trend began. Hatches were stable until 1991 when they suddenly doubled and continued to increase thereafter (67 hatches in 1999). This suggests two different populations may be involved.

Movements of this species are ill defined. There are scant band recovery data for Hooded Mergansers. Because they are carnivorous (Dugger et al. 1994), they are not bait trapped.

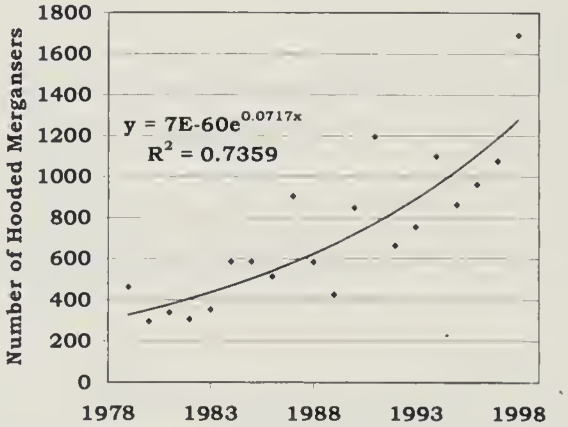

FIG. 3. Numbers of Hooded Mergansers counted on 21 Christmas Bird Count circles in Massachusetts, 1979–1998.

Moreover, they do not concentrate in flocks during the summer or fall, making other forms of capture difficult. During 1989–1998 we banded more than 8700 ducks captured by airboat nightlighting including 5615 Wood Ducks, but only 6 Hooded Mergansers (Heusmann, unpubl. data). Most banding of Hooded Mergansers in the Northeast has been of incubating females in nest boxes. Eighty percent of the band recoveries from these birds were recovered in Atlantic Coast states from New Jersey to Florida (Dugger et al. 1994) but adult male waterfowl may winter farther north (Brodsky and Weatherhead 1984). The increase in Hooded Mergansers in Massachusetts CBCs likely reflects an increase in numbers in the Northeast with birds moving down from more northern latitudes, but may also include more birds hatched in Massachusetts. Some of the population increase may be attributed to improved habitat with maturing forests and an increase in nest cavity trees (Heusmann and Bellville 1982). Beaver (*Castor canadensis*) populations have also increased in the Northeast (Southwick Associates 1994) resulting in more small, wooded, ponds favored by Hooded Mergansers.

Changes in hunting season regulations may also have affected Hooded Merganser numbers. From 1969 to 1986, hunting seasons in the Atlantic Flyway were 50 days with a daily bag limit of 1 Hooded Merganser. During that period harvests averaged 21,000, but when seasons were restricted to 30 days from 1988–1993, the average harvest dropped to 15,800 (Serie et al. 1999). Hunting seasons were increased to 50 days by 1995 and to 60 days in 1997. Hooded Merganser harvests since 1995 in the Atlantic Flyway have averaged 29,150 (Serie et al. 1999). This may be an indication of increased Hooded Merganser populations, increased harvests related to longer seasons, or a combination of the two. In a southeastern Missouri study, Dugger and coworkers (1999) found no significant difference between Hooded Merganser survival rates and annual harvest. It remains to be seen if Hooded Merganser populations in the Northeast will continue to increase despite longer duck hunting seasons.

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Wilson Bull., 112(3), 2000, pp. 416–417

Northern Harrier Predation of White-faced Ibis

James W. Rivers[1,2]

ABSTRACT.—The Northern Harrier (*Circus cyaneus*) is a widespread raptor that preys mainly upon small mammals and, to a lesser extent, birds. Most published accounts of harrier food habits report the majority of avian prey items are passerines with few large (> 500 g) birds taken. In fall 1999, I observed a Northern Harrier that appeared to have attacked and killed a White-faced Ibis (*Plegadis chihi*) foraging in a playa wetland in Meade County, Kansas. Field observations of the harrier, in addition to physical evidence, suggest the attack was on an apparently healthy individual that did not have any obvious physical deformities. Northern Harriers appear to attack and kill White-faced Ibis and may prey on large birds more often than reported previously. *Received 26 Jan. 2000, accepted 31 March 2000.*

At 09:50 (CST) on 25 September 1999, I flushed a Northern Harrier (*Circus cyaneus*) in female or juvenile plumage from vegetation surrounding a shallow (ca 10 cm deep) playa wetland in Meade County, Kansas. After flushing the harrier from the vicinity of the playa, I examined the area it left and discovered the fresh remains of a White-faced Ibis (*Plegadis chihi*). The ibis was in moderate cover of moist-soil vegetation (mainly *Polygonum bicorne* and *Echinochloa colona*); its feathers and blood were scattered within a 1 m radius surrounding the carcass. The ibis was decapitated and muscles were removed cleanly from the anterior end of the vertebral column and both humeri. The right side of the pectoralis muscle was completely removed but the left side was intact. The carcass was eviscerated; parts of the intestine were nearly 1 m from the carcass. The heart was intact and the wings and legs were still attached to the carcass. The bill, wings, and legs lacked obvious physical deformities that may have contributed to its capture. The fourth digit on the left foot appeared to have been previously broken but had healed and likely had no role in the attack.

Several clues suggest the ibis was killed shortly before I discovered it. The stomach was filled with invertebrate prey (e.g., Anisoptera, Notonectidae, Gyrinidae) suggesting it had been foraging shortly before it died. The presence of soft-bodied Anisopteran larvae in the stomach suggests the bird was discovered immediately after it was killed because soft-bodied invertebrates are quickly digested in the stomach (Swanson and Bartonek 1970, Rundle 1982), even after death of the predator (Dillery 1965). In addition, the carcass was fresh, had not undergone decomposition, and lacked necrophilic invertebrates (e.g., Dipteran larvae).

To my knowledge, this is the first report of Northern Harrier predation on a White-faced Ibis (Ryder and Manry 1994; MacWhirter and Bildstein 1996; E. Kelchlin, pers. comm.). Northern Harriers are believed to prey upon nestling ibis in rookeries (E. Kelchlin, pers. comm.), but predation of a juvenile or adult ibis (age of the ibis was unknown) is undocumented. Based on the evidence, it seems plausible that the harrier I observed killed the ibis because Northern Harriers have been reported to take prey as large as 1 kg (Barnard et al. 1987, MacWhirter and Bildstein 1996), a range that includes White-faced Ibis (Ryder and Manry 1994).

An alternative interpretation of my observation is that the ibis was killed by another predator and was scavenged by the harrier. This explanation is unlikely because scaveng-

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ing by harriers is thought to be restricted to stressful weather periods (K. Bildstein, pers. comm.). Temperatures in Meade County were similar to the 51 year average for 25 September and several days prior, indicating that conditions were not stressful enough to induce scavenging. Therefore, all evidence suggests the harrier attacked and killed the White-faced Ibis the morning of 25 September. Moreover, this observation indicates that White-faced Ibis are likely prey items of Northern Harriers and suggests this raptor takes large avian prey more commonly than previously reported (Barnard et al. 1987, Collopy and Bildstein 1987, MacWhirter and Bildstein 1996).

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Comparable Reproductive Success at Conifer Plantation and Non-plantation Nest Sites for Cooper's Hawks in Wisconsin

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ABSTRACT.—Some birds that attempt to nest in habitats such as conifer plantations may experience lower reproductive success and diminished fitness in comparison to conspecifics in other habitats, rendering such habitats sinks or ecological traps. We did not detect significant differences between conifer plantation and non-plantation nests in terms of clutch size, number of bandable young per nest, or nest success for Cooper's Hawks (*Accipiter cooperii*) in Wisconsin during 1980–1998. Pine plantations contributed recruits to subsequent breeding generations in proportion to their productivity of bandable nestlings. Conifer plantations in Wisconsin also contained nesting densities and productivity indices for Cooper's Hawks that are among the highest reported for the species. Thus, conifer plantations in Wisconsin are neither ecological traps nor population sinks for nesting Cooper's Hawks. *Received 4 Jan. 2000, accepted 22 April 2000.*

Some breeding bird species may be poorly adapted to compositionally, structurally, or otherwise novel, exotic, or human-modified

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habitats such as conifer plantations (Cody 1985). Birds that attempt to nest in these novel and potentially inferior habitats–hence possible "sinks" or "traps"–may experience lower reproductive success and fitness in comparison to conspecifics in other habitats (Gates and Gysel 1978); other species may of course be better adapted to such habitats (Bird et al. 1996).

Many investigators studying habitat use among nesting raptors (Bird et al. 1996, Newton 1996, Boal and Mannan 1999) and other breeding bird species (Bielefeldt and Rosenfield 1994) have felt it useful to delineate several types of human-altered environments, including conifer plantations, that have been characterized, "somewhat emotively" (Curry 1991), as biological deserts or biologically desolate habitat (Capen 1979). Conifer plantations, principally high density monocultures of white and/or red pine (*Pinus strobus, P. resinosa*), occupy about 240,000 ha in Wisconsin (Spencer et al. 1988). Most of these plantations are less than 60 yrs old and many are located in the predominately agricultural landscape of southern Wisconsin where native conifers were absent historically. These plantations differ in physiognomy, composition, and other respects from the state's deciduous woodlands and mixed conifer-hardwood forests (Curtis 1959).

We were unable to detect a link between pairs' reproductive successes and the presumptive quality of nest sites as indexed by consistency of use (Rosenfield and Bielefeldt 1999) for Cooper's Hawks (*Accipiter cooperii*) in Wisconsin. Here we extend our analysis of site effects by comparing several measures of breeding success (including recruitment) at Cooper's Hawk nests in conifer plantations versus other woodlands in Wisconsin.

METHODS

Conifer plantation and non-plantation nests used in these analyses in Wisconsin, 1980–1998, were discovered before egg-laying by listening for dawn vocalizations. The utility of finding nesting pairs using this method is provided by Rosenfield and Bielefeldt (1991), Stewart and co-workers (1996), and Rosenfield and others (1991, 1996). We also located partially constructed nests during intensive ground searches during the pre-incubation stage (ca. mid-March through late April; Bielefeldt et al. 1998). Thus we are able to examine productivity, including recruitment to subsequent breeding generations, without adjusting for the biases that might have resulted from excluding breeding attempts that failed prior to discovery (Mayfield 1961, Steenhoff and Kochert 1982). We separated nests into 100 spatially and statistically independent sites and 243 non-independent nests located at the same 100 sites in subsequent years.

We regard the definition of conifer plantation as self-evident. Other woodland nest site habitats include purely deciduous stands (typically oaks, *Quercus* spp.), naturally occurring coniferous stands (mainly pines, *Pinus* spp.), and mixed conifer-hardwood stands. For more description of nesting habitats see Bielefeldt and co-workers (1998). We climbed nest trees during mid-to late incubation to count eggs. We counted and banded nestlings with U.S. Fish and Wildlife Service aluminum bands at the mid-nestling stage (ca 16 days of age). We considered nests successful when one or more nestlings reached bandable age. Data on recruits were derived from hawks banded as nestlings and captured as breeding birds in later years (Rosenfield and Bielefeldt 1999). We accepted statistical significance at the 0.05 level. Statistical analyses were performed on SYSTAT, version 5 for windows (Wilkinson 1992).

RESULTS

Although we did not detect any significant differences between plantation and non-plantation nests in terms of clutch size, number of bandable young per nest, or nest success, productivity for all respects was marginally greater at conifer plantation nests versus non-plantation nests in both independent and non-independent data sets (Table 1).

Of 1003 nestlings in 343 nests in our non-independent data set, 437 (44%) were banded at plantation nest sites. Among 16 recruits, 6 (38%) were raised in plantations and 10 (62%) in non-plantation nests. With our sample, it appears that pine plantations in Wisconsin contributed recruits to subsequent breeding generations in proportion to their productivity of bandable nestlings. Of the 16 recruits 6 (3 males, 3 females) eventually nested in conifer plantations. Two recruits switched habitat types between natal sites and breeding sites: a male raised in a mixed conifer-hardwood stand later bred in a purely deciduous stand, and a female from a mixed conifer-hardwood site bred in a pine plantation.

DISCUSSION

We did not detect statistically significant differences in clutch size, nest success, or number of bandable young per nest at Cooper's Hawk nests in conifer plantations versus

TABLE 1. Mean reproductive success (SE; n) at independent and non-independent Cooper's Hawk nests in conifer plantations versus other woodland habitats in Wisconsin, 1980–1998.[a]

	$\bar{x}$ clutch size	$\bar{x}$ no. bandable young	Nest success
Independent			
Non-plantation	4.2 (0.11; $n = 51$)	2.8 (0.22; $n = 71$)	77% ($n = 71$)
Plantation	4.3 (0.15; $n = 25$)	3.3 (0.32; $n = 29$)	86% ($n = 29$)
Non-independent			
Non-plantation	4.2 (0.07; $n = 125$)	2.8 (0.43; $n = 201$)	77% ($n = 201$)
Plantation	4.4 (0.07; $n = 107$)	3.1 (0.12; $n = 142$)	81% ($n = 142$)

[a] No statistical differences between non-plantation and plantation nests for independent ($t = 0.44$, 74 df, $P > 0.05$) and non-independent (Mann-Whitney $U = 7489$, $n = 106$ and 124, $P > 0.05$) categories of clutch sizes, for independent ($t = 1.46$, 98 df, $P > 0.05$) and non-independent (Mann-Whitney $U = 15{,}539$, $n = 141$ and 200, $P > 0.05$) categories of bandable young; nor for non-plantation and plantation nests for independent ($\chi^2 = 0.98$, 1 df, $P > 0.05$) and non-independent ($\chi^2 = 0.75$, 1 df, $P > 0.05$) categories of nest success.

nests at non-plantation sites, despite the compositional, structural, and other novel ecological attributes of conifer plantations as breeding bird habitat. Raptor biologists and other avian ecologists often must rely upon these readily gathered indices of productivity (Table 1) because of the difficulty of collecting data on recruitment. Not only do these commonly used indices fail to show significant differences for Cooper's Hawks nesting in conifer plantations versus non-plantation habitats, but our data on 16 recruits also fail to reveal differences in fitness of Cooper's Hawks breeding in plantation versus non-plantation nest sites.

Conventional measures of productivity (Table 1) in both plantation and non-plantation habitats in Wisconsin (1980–1998) were as high as those reported for northeastern North America prior to the introduction of DDT in 1945 (Henny and Wight 1972). Conifer plantations in Wisconsin exhibit nesting densities and productivity indices that are among the highest reported for the Cooper's Hawk (Rosenfield and Bielefeldt 1993, Rosenfield et al. 1995; Table 1). Although Van Horne (1983) showed that seemingly high breeding densities may not be an adequate indicator of habitat quality as defined by reproductive success, this was not the case with plantation habitats for Cooper's Hawks in Wisconsin.

Conifer plantations may attract nesting Cooper's Hawks, as seemed to have occurred on one Wisconsin study area where all of 9 known nests (in two years) were found within plantations that provided only ⅓ of available woodland habitats (Rosenfield et al. 1995). However, plantation nests in Wisconsin (Rosenfield et al. 1995, this study) did not show diminished reproductive success. Novel habitats such as conifer plantations may present unusable or reproductively inferior sites for some breeding bird species (Cody 1985) but this does not seem to be the case for Cooper's Hawks nesting in conifer plantations in Wisconsin. Eurasian Hobbies (*Falco subbuteo*) had comparable nesting densities and conventially measured reproductive successes in natural habitats compared to birds breeding in 8–12 year old short-lived poplar (*Populus* spp.) plantations in Italy (Sergio and Bogliani 1999). Other species or local populations presumably will show individualistic or plastic responses to novel habitats in terms of occupancy, density, reproductive success, and hence habitat quality. In the absence of demographic data, there thus seems to be no *a priori* reason to suppose that a category or a patch of purportedly novel habitat is or is not a low-quality habitat, a population sink, or an ecological trap for any particular species.

The array of raptors and other birds using or colonizing conifer plantations within and outside their previously recognized breeding ranges in Wisconsin (Bielefeldt and Rosenfield 1992, 1993, 1994; Trexel et al. 1999; Rosenfield et al. 1998) and elsewhere (Newton 1996, Robinson 1996, Hunt and Flaspohler 1998) provides many opportunities to test these precepts (Boal and Mannan 1999, Bielefeldt and Rosenfield 2000, Whitt et al. 1999, Flaspohler et al. 2000).

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Ruby-throated Hummingbird Death by Common Burdock (*Arctium minus*)

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ABSTRACT.—A Ruby-throated Hummingbird (*Archilochus colubris*) that had become entangled and died in the flowers of a common burdock (*Arctium minus*) was found 12 August 1999 in Cambria County, Pennsylvania. *Received 10 Dec. 1999, accepted 8 March 2000.*

The carcass of a Ruby-throated Hummingbird (*Archilochus colubris*) was discovered on 12 August 1999 adhered to the burs of common burdock (*Arctium minus*) flowers in Cambria County, Pennsylvania (40° 37′ N, 78° 50′ W). Common burdock is an exotic plant species introduced from Europe (Strausbaugh and Cole 1977) that has become widely established in crop and pasture lands. The plant produces reddish, tubular flowers and is well-known for the burs (a dense layer of hooked bristles) that occur on its fruiting heads (1.5–3.0 cm diameter).

The bird was salvaged under appropriate state and federal permits and, upon closer examination, was determined to be an immature female. Our basis for identification includes the presence of numerous bill corrugations, plumage characteristics (buffy white throat lacking reddish feathers; outer rectrices tipped with large areas of white), and measurements (exposed culmen = 17.6 mm, unflattened wing chord = 46.0 mm, maximum tail length = 24.0 mm; Leberman 1972, Ortiz-Crespo 1972, Baltosser 1987).

The flower clusters of the burdock were nearly mature; most were at least partially open with exposed red/purple flowers. We have found no reports of hummingbird feeding upon common burdock, although the propensity of Ruby-throated Hummingbirds to visit reddish flowers is well known (Robinson et al. 1996; but see Miller and Miller 1971). The position of the hummingbird suggests that it attempted to perch, rather than feed upon the exposed cluster of flowering heads and became caught. Ventral body, tail, and several primary flight feathers were entangled or impaled by the hooked bristles.

Several recent reports suggest that this is not an isolated incident. Wilkinson (1999) summarized published reports describing the physical dangers posed by exotic vegetation (including burdock) to native birds and bats. Likewise, Brewer (1994) and McNicholl (1994) report on burdock caused avian deaths, including hummingbirds, nuthatches, kinglets, warblers and other taxa. It seems clear that although burdock caused avian mortality may be uncommon, it is not rare. Thus, we must add the risk of physical entrapment of native birds to the list of threats posed by exotic vegetation.

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Attack on Chestnut-bellied Euphonia Nestlings by Army Ants

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ABSTRACT.—I report some observations of a Chestnut-bellied Euphonia (*Euphonia pectoralis*) nest in a lowland Atlantic Forest of southeastern Brazil during the early nestling period. During 7.5 hours of observations, the nest was attended 46.3% of the time, 45.6% by the female and 0.7% by the male. Unattended periods lasted 16–38 min. Parents visited the nest most of the time together at 36–59 min intervals. There were 1.06 feeding visits per nestling per hour. The two nestlings in the nest ended up preyed upon by army ants (*Labidus praedator*, Ecitoninae). The low height of the nest (0.8 m) may have facilitated its detection by the ants. *Received 17 Feb. 2000, accepted 11 May 2000.*

The Chestnut-bellied Euphonia (*Euphonia pectoralis*) is a medium-sized (length 11 cm, weight 16 g; Isler and Isler 1987), sexually dimorphic tanager that occurs in southeast South America. It inhabits forests and their edges, being especially common in humid forest areas (Isler and Isler 1987, Ridgely and Tudor 1994). Its breeding behavior is poorly known; the available information comes from scattered observations on a few nests (Bertoni 1919, Snethlage and Schreiner 1929, Anjos and Schuchmann 1999). Here, I report some observations made on a nest discovered early in the nestling period, and that ended up preyed upon by army ants (*Labidus praedator*, Ecitoninae).

The observations were carried out at the Saibadela Research Station (24° 14′ S, 48° 04′ W; 70 m a.s.l.) at Parque Estadual Intervales, a 49,000 ha reserve located in São Paulo state, southeastern Brazil. The region received a mean annual rainfall of 4216 mm between 1994–1996. Although rains are evenly distributed throughout the year, showers are more intense and frequent October to March, which is also the hottest period. Old-growth forest (sensu Clark 1996) predominates in the site. The understory is open and the canopy averages 25 m tall with a few emergent trees reaching 30 m (Almeida-Scabbia 1996). The Chestnut-bellied Euphonia is a common resident bird at Saibadela (Aleixo and Galetti 1997).

The dome-shaped nest was discovered 9 October 1995 and contained two newly-hatched young and one unhatched egg. The nest was at the base of an epiphytic bromeliad, on the side of a tree trunk growing in the forest interior, 80 cm above the ground. The outside of the nest was composed of mosses and

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a tangle of bromeliad rootlets on its top, and measured 12 (height) × 15 (width) cm. The nest entrance, partially camouflaged by an overhanging awning, measured 3.2 (height) × 3.5 (width) cm. The nest differed in two aspects from a nest found by Anjos and Schuchmann (1999): the entrance was closer to the top than to the bottom of the nest and no cone-shaped plant material was attached to it.

Five observation sessions (0.5–2.5 h each; 7.5 h total) were distributed throughout the day between 10–14 October from a concealed position 10 m from the nest. Overall the nest was attended for 46.3% of the time, 45.6% by the female and 0.7% by the male. Unattended periods lasted 16–38 min [mean = 21.7 ± 8.5 (SD), $n = 6$]. Supporting my impression that the young had recently hatched, the female brooded them (Sargent 1993) for bouts that lasted 17–73 min (31.0 ± 23.5 min, $n = 5$). The presence of the male in the nest was very brief (0.5 ± 0.1 min, range 0.3–0.6 min, $n = 6$), probably only long enough to deliver food to the nestlings.

Parents visited the nest most of the time together (seven of nine visits, the remaining two were by the female alone) at 36–59 min intervals (45.0 ± 9.1 min, $n = 5$). There were 1.06 feeding visits per nestling per hour, similar to that reported for other euphonias (0.75–1.33; Skutch 1989). As observed for other euphonias (e.g., White-vented Euphonia, *E. minuta,* Skutch 1972; Yellow-throated Euphonia, *E. hirundinaceae,* Sargent 1993) the male Chestnut-bellied Euphonia preceded his mate in feeding the young in six of the seven joint visits to the nest. After the male completed his feeding duty, he perched on a suspended root 1.5 m from the nest and followed the female closely half her way to the nest. When she entered the nest, the male turned in midair and returned to the perch. Such escorting flight has been observed in a variety of birds (Skutch 1981), including the Yellow-throated Euphonia (Sargent 1993). Unlike that species, the female Chestnut-bellied Euphonia was never observed escorting her mate to the nest.

On the morning of 15 October I observed both parents making a series of unsuccessful attempts to enter the nest. Upon inspecting the nest chamber I found both nestlings dead, completely covered by workers of the army ant (*Labidus praedator*). Attacks on bird nestlings by ants seem to be rare, being more common in open than in forested areas. Oniki (1979, 1985) reported only 14 of 4089 nests depredated by ants in Manaus and Belém in the Brazilian Amazon. All 14 nests were located in open terrains. Fire ants (*Solenopsis invicta,* Myrmicinae), an inhabitant of open areas, are the most frequent nest attacking ant reported (Skutch 1931, 1951, 1986; Dickinson 1995 and references included). Other instances involve ants of the genus *Monomorium* (Myrmicinae; Parker 1977). Although Skutch (1986) thought that army ants rarely harm bird eggs or nestlings, Schneirla (1956 in Hölldobler and Wilson 1990) observed nestlings killed by the army ant *Eciton burchelli* (Ecitoninae). Gotwald (1995) classifies *L. praedator* as an indiscriminate predator that forages day and night taking a variety of arthropods, carcasses of dead animals, and vegetable material. As far as I know this is the first report of *L. praedator* preying upon nestling birds. The low height of the nest (0.8 m compared to 2–4 m of other reports; Isler and Isler 1987, Anjos and Schuchmann 1999) may have facilitated its detection by foraging ants. I observed worker *E. burchelli* climbing 8 m up a tree to attack a wasp's nest. Therefore, there is opportunity for the nomadic and highly carnivorous army ants to find and attack bird nests in tropical forests. The paucity of such events in the literature might only reflect the rarity with which they are witnessed in nature.

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Neophobia by the Lesser-Antillean Bullfinch, a Foraging Generalist, and the Bananaquit, a Nectar Specialist

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ABSTRACT.—Generalist birds are thought to be less neophobic than specialists, but the dietary difference is often confounded by differences in experience and food availability. We conducted field tests with an artificial nectar source on a foraging generalist [Lesser-Antillean Bullfinch (*Loxigilla noctis*)] and a nectarivorous specialist [Bananaquit (*Coereba flaveola*)] in Barbados. Both species are equally opportunistic and tame on this island. Bullfinches arrived first at the feeding stations and showed a shorter latency to feed in the tests than did Bananaquits, suggesting that differences in specialization lead to the differences in neophobia predicted by ecological plasticity. *Received 1 Nov. 1999, accepted 5 March 2000.*

Dietary generalists exploit a large variety of food types and are consequently more likely than specialists to encounter novel stimuli associated with food. Greenberg (1984, 1990, 1992) has shown that generalist warblers (Bay-breasted Warbler, *Dendroica castanea*) and sparrows (Song Sparrow, *Melospiza melodia*) feed more rapidly in the presence of novel objects than do more specialized species of their genus (Chestnut-sided Warbler, *D. pensylvanica*; Swamp Sparrow, *M. georgiana*). In many cases, the generalist/specialist continuum is confounded by opportunism/conservatism. In warblers, for instance, the neophilic Bay-breasted Warbler is the *Dendroica* species that displays the largest number of opportunistic foraging behaviors when it migrates to its wintering areas in Central America (Greenberg 1979). Separating generalism from opportunism would be useful in teasing out the respective contributions of

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these variables to ecological plasticity. Two tame, opportunistic species of the West Indies Passeriformes offer this possibility. In Barbados (Bond 1985, Lefebvre 1996) and several other West Indian islands (Pinchon 1964, Devas 1970, Voous 1983), the Bananaquit (*Coereba flaveola*) and the Lesser-Antillean Bullfinch (*Loxigilla noctis*) routinely feed at provisioned sources of artificial nectar. The birds often perch on the sides of glasses, cups, and sugar bowls and are deliberately attracted to hotels and restaurants by dishes of dissolved sugar (Lefebvre 1996). Although matched for size, abundance, tameness, and opportunistic response to sugar provisioning, as well as being closely-related according to Sibley and Ahlquist's (1990) molecular classification, the species show a striking difference in feeding morphology and diet breadth. The Bananaquit has a long, brush-like tongue and a curved bill that are morphologically specialized for feeding from flowers (Raffaele 1983), while the Lesser-Antillean Bullfinch has a short, thick bill that allows it to crack open seeds (Pinchon 1964). In Barbados, the bullfinch, but not the Bananaquit, routinely forages with other granivorous and omnivorous birds that exploit food left by humans (Dolman et al. 1996). If generalism has effects on neophobia that are independent of both tameness and opportunism, bullfinches should respond more rapidly than Bananaquits to a standard feeding test (Greenberg 1984) presented in the field.

The experiment was conducted during July and August 1999 at five sites (separated by at least 20 m) on the grounds of the Bellairs Research Institute of McGill University, St-James, Barbados. We used the procedure developed by Greenberg (1984) to compare the latency to feed in trials that randomly feature either a novel object or no novel object close to a patch of accessible food. The procedure also incorporated a measure of tameness, because latency is calculated as return time after interruption by the experimenter of a bird's initial feeding bout. Before each set of trials, a dish containing 50 ml of a 30% sucrose solution (typical for flowers) was placed on an elevated surface (wall, table, etc.) at each site, approximately 1 m off the ground, until both species fed within 5 min after the food was presented. This familiarization phase took an average of 2 days. On each of three matched pairs of trials conducted on different days, the experimenter then presented a dish filled with 50 ml of 30% sucrose at one of the five sites. The latency of the birds to approach the dish was recorded. If the birds did not feed within 20 min, the trial was terminated and repeated the following day. Once a bird started to feed, the experimenter approached the feeding station at a constant, slow pace, and randomly (determined by coin flipping) initiated either a control trial (rotating the food dish) or a novel object trial (rotating the dish and placing one of three objects 2 cm from the dish). A marker was dropped at the experimenter's location when the bird interrupted its initial feeding in the approach phase; distance between the marker and the dish was measured at the end of each trial. On novel object trials, the coin was tossed again to determine which of the three novel objects would be used. The novel objects were three straws of different colors sticking vertically from a ball of paper, three springs approximately 2.5 cm in diameter and 10 cm long, and a handful of curly, frayed paper. Each object was mounted on a piece of 8 × 8 cm cardboard. Latency to feed from the dish was recorded for all trials. Birds were given a maximum of 20 min to return to the dish in both types of trials; a failure to return was scored as a latency of 1201 sec. One trial was conducted per day at each of the five sites, with a total of six testing days per site (three controls, three novel objects). During the trials, the experimenter was initially located 15 m away from the feeding station to allow the birds to feed undisturbed.

Bullfinches and Bananaquits visited the food patch together on 26 of the 30 trials. On these trials, a single bird from each species would normally feed without interference from opposite sides of the dish. On two trials, the dish was visited only by a bullfinch, while on two trials, only a Bananaquit fed. Bullfinches arrived at the food first on 20 of the 30 trials, while Bananaquits arrived first on 8 trials (Fig. 1A; difference between species: $\chi^2 = 5.14$, 1 df, $P < 0.05$); the two species arrived together on the remaining two trials. After experimenter interruption, bullfinches returned faster than Bananaquits (Fig. 1C; ANOVA, Systat 8.0: $F_{1,8} = 12.217$, $P = 0.008$; latencies log transformed for normalization), and both species were somewhat slower to re-

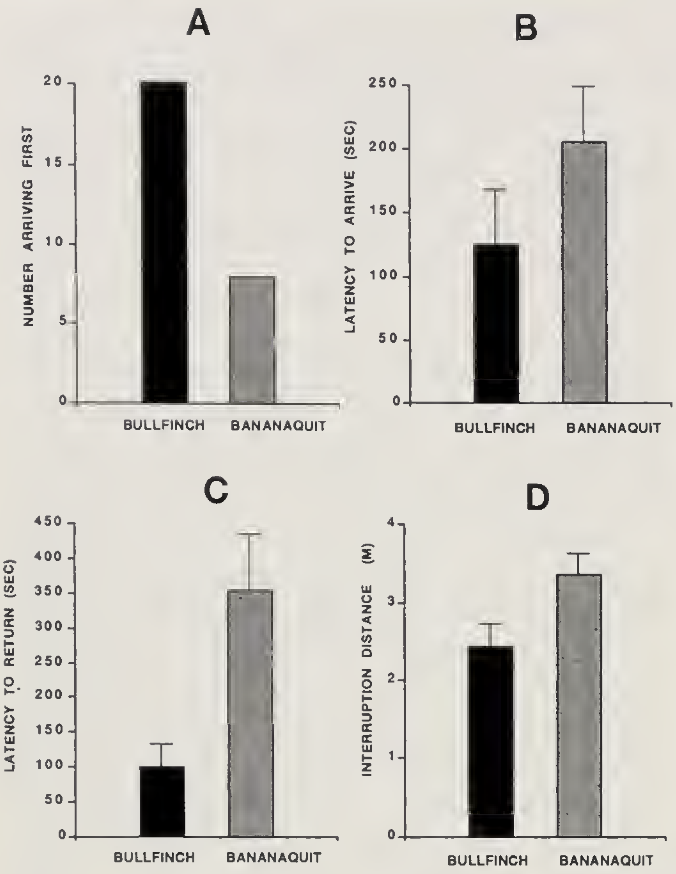

FIG. 1. Response to the different phases of the test in Lesser-Antillean Bullfinches and Bananaquits. A. number of trials in which each species arrived first; B. latency (sec) to initial feeding before interruption; C. latency (sec) to return after interruption; D. distance (m) of experimenter when initial feeding was interrupted. Means for B, C, and D are averaged over replicates.

turn in the presence of novel objects (ANOVA: $F_{1,8} = 4.973$, $P = 0.056$). Neither the replicate effect nor any of the interaction effects were significant. The two species did not differ significantly in their latency to arrive when the food was put out (Fig. 1B; $F_{1,8} = 1.361$, $P > 0.05$), nor in how close they allowed the experimenter to approach (Fig. 1D; $F_{1,8} = 2.885$, $P > 0.05$).

Overall, the results support the prediction that the more generalized bullfinch will more rapidly approach a novel feeding situation than the more specialized Bananaquit. Behaviors typical of neophobia (jumping, flitting) were often observed near the novel objects by Bananaquits, but not bullfinches. In addition, at four out of the five sites, Bananaquits failed to return within the 20 min time limit of the trial with at least one of the novel objects, while bullfinches always returned. This difference was not sufficient to support the strongest prediction of neophobia tests: a significant species by patch type interaction. Only the main effects of species and patch type were significant, suggesting that bullfinches respond more quickly than Bananaquits whether or not the food has a novel object next to it. This is consistent with the fact that bullfinches arrived first at the patch more often than did Bananaquits. The interspecific difference is difficult to attribute to motivational or other contextual factors because the food we used biased the test in favor of Bananaquits.

Our tests of neophobia involved the proximity (and often, direct intervention) of a human experimenter, just as new feeding opportunities in the field are often related to anthropogenic modification of natural habitats. Tameness is likely to be confounded with opportunism as well as generalism in many situations where ecological plasticity plays a role. In cases where the generalist is also more tame and opportunistic than the specialist, we can expect interspecific differences to be stronger than the ones reported here because the confounded effects presumably are cumulative. Our study demonstrates that in the absence of such interactions, a difference in diet breadth and morphological specialization is sufficient to lead to the overall behavioral differences predicted by the ecological plasticity model (Greenberg 1990).

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Belding's Savannah Sparrows Eat Eggs From Live Fiddler Crabs

Catherine E. deRivera[1]

ABSTRACT. —On 17 occasions in Chula Vista, California, at least one Belding's Savannah Sparrow (*Passerculus sandwichensis beldingi*) was observed chasing egg-carrying female fiddler crabs (*Uca crenulata*) and pecking eggs from ones it caught. Sparrows did not eat any part of the adult crab while eating the eggs. A fledgling learned this novel hunting technique after accompanying its parent for a month. *Received 29 December 1999, accepted 1 May 2000.*

Feeding innovations have been reported for numerous species of birds (Lefebvre et al. 1997). Perhaps the best known example is the opening of milk bottles by Great Tits (*Parus major*; Fisher and Hinde 1949). Here I report a feeding innovation by Belding's Savannah Sparrows (*Passerculus sandwichensis beldingi*) in which the birds ate eggs from live California fiddler crabs (*Uca crenulata*) but did not eat the adult crabs.

Belding's Savannah Sparrow is an endemic subspecies that inhabits the remaining coastal salt marshes in southern California and Baja, Mexico, and is on California's state endangered species list (Bradley 1973). Savannah Sparrows often forage in the littoral zones where they eat a wide variety of arthropods; in winter they supplement their diet with the growing tips of marsh vegetation (Massey 1979, Wheelright and Rising 1993, Powell and Collier 1998).

I observed an adult Belding's Savannah Sparrow eating fiddler crab eggs on the D Street Fill mudflat in Chula Vista, California, where the Sweetwater River empties into San Diego Bay. This mudflat is an extension of the Sweetwater Marsh National Wildlife Refuge. The predominant vegetation is pickleweed (*Salicornia virginica*), which is typically found in habitat used by Belding's Savannah Sparrows and California fiddler crabs (Powell 1993; deRivera, unpubl. data). I observed 1600 m^2 of the mudflat.

Fiddler crab eggs are readily available to predators throughout the fiddler crab breeding season, from May through August. Female California fiddler crabs carry large clutches of eggs for approximately 16 days (deRivera 1999). Although female crabs spend much of their incubation time underground, some of the egg-carrying females surfaced on 85% of the breeding-season days. More than 161 females with eggs were seen on the surface over 35 observation days in 1999. Egg-carrying females were easy to spot because they held their abdomens in a characteristic lowered position and their eggs protruded beyond their undersides.

I noticed a Belding's Savannah Sparrow chasing an egg-carrying fiddler crab on 22 June 1999. I looked for sparrows on 20 nonconsecutive days during the remainder of the

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fiddler crab breeding season. A Belding's Savannah Sparrow chased up to five egg-carrying females on each of 17 days in June and July (n = 49 chases). Sparrows successfully ate eggs from females after over 35% of the chases (≥ 18/49; not all outcomes were observed). Only 12% of the female crabs I observed had eggs, but sparrows never chased male crabs or eggless female crabs.

Fiddler crabs would flee sparrows but eventually either turned to face them or entered a burrow. The sparrow pecked at crabs entering burrows. When a sparrow successfully retrieved a crab from a burrow, the crab faced the sparrow. In each of 18 cases in which a crab faced a sparrow, the sparrow repeatedly pecked at the crab's exposed eggs. Once I located the female crab after the sparrow fed. This female was undamaged but only had 59 eggs left. The female crab was 14.5 mm wide and would typically carry an average of 3725 eggs. I observed no damage to adults from afar after 17 other successful chases, but noted that these females had reduced egg masses when the sparrow finished feeding.

A fledgling sparrow started accompanying the adult on 7 July. It ran behind its parent and begged. The adult fed eggs to the fledgling after each peck at the crab. The fledgling chased egg-carrying fiddler crabs independently from the parent by 10 August, apparently having learned by observing its parent.

Birds frequently innovate feeding methods and other behaviors. Feeding innovations often entail exploiting a novel food source, such as Storm Petrels (*Oceanites oceanicus*) feeding on decaying whale fat (Payne et al. 1983). Alternatively, a bird uses a new technique for capturing, gathering, or storing food, such as Cetti's Warblers (*Cettia cetti*) catching insects using techniques typical of flycatchers, or Gila Woodpeckers (*Melanerpes uropygialis*), a non-storing species, storing acorns (MacRoberts and MacRoberts 1985, Hill 1993). Here, Belding's Savannah Sparrows exploited a new food source and used a new hunting method. Furthermore, the behavior of eating eggs from female fiddler crabs is noteworthy because the sparrows did not damage the adult crabs.

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Whimbrel Attacked by a Peregrine Falcon and Killed by a Common Raven in Northern California

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ABSTRACT.—A Peregrine Falcon (*Falco peregrinus*) was observed stooping on a Whimbrel (*Numenius phaeopus*) that was eventually attacked by a nearby Common Raven (*Corvus corax*). This incident reinforces the idea that ravens are opportunistic and intelligent predators capable of kleptoparasitizing large prey items. *Received 22 Oct. 1999, accepted 3 March 2000.*

Common Ravens (*Corvus corax*) are large birds (920–1560 g) that feed principally on carrion but also take nestling birds, eggs, and small rodents (Madge and Burn 1994). Goodwin and Gillmore (1976) stated that ravens readily recognize and attack sick or injured birds that are too large to be preyed upon normally. Otto (1998) described an incident in which a Common Raven attacked a snowshoe hare (*Lepus americanus*) escaping from an American martin (*Martes americana*). J. Dunk (pers. comm.) observed a raven chase an injured Black Scoter (*Melanitta nigra*) in the Arcata Bottoms, California for about 0.5 km before abandoning the chase. Klicka and Winker (1991) observed a raven attack and kill a nesting Black-legged Kittiwake (*Rissa tridactyla*; 367–399 g; Gabrielson et al. 1987) that would not abandon its nest. Parmelee and Parmelee (1988) also observed two Common Ravens attack and kill two adult kittiwakes that were roosting among several hundred kittiwakes. Ravens have been observed attacking and killing adult birds including ptarmigan (*Lagopus* sp.), puffin (*Fratercula* sp.), and partridge (*Perdix* sp.; Madge and Burn 1994).

Whimbrel (*Numenius phaeopus*) eggs and young are normally preyed upon by ravens but adults, which typically range in mass from 310–493 g, have not been documented as raven prey (Skeel and Mallory 1996).

On 6 May 1999, at approximately 11:00 PST, I observed a Peregrine Falcon (*Falco peregrinus*) pursuing a Whimbrel in a pasture north of Humboldt Bay, Arcata, California (40° 52′ N, 124° 7′ W). The area consists of 1800 hectares of pasture land that serves as an important site for non-breeding shorebirds (Colwell and Dodd 1995, Harris 1991). Falcons also frequent this area year round but are more abundant during the non-breeding season (Harris 1991). Using 10 × 50 binoculars, I observed the falcon repeatedly stooping from an elevation of 5–7 m on a Whimbrel hunkered in grass approximately 20 m from me. A Common Raven was also on the ground approximately 3 m from the Whimbrel. The falcon stooped the Whimbrel eight times before the raven jumped on the Whimbrel's back and began pecking its head. The falcon stooped on both raven and Whimbrel one more time, causing the raven to slip off the Whimbrel's back, then flew east and was not observed again. With wings spread, the Whimbrel faced the raven. The raven attacked three more times by jumping on the Whimbrel and repeatedly striking the back of its head. Each attack lasted approximately five seconds. After the fourth attack, the Whimbrel attempted to fly but the raven pursued and prevented the Whimbrel from flying by nipping at the Whimbrel's tail and legs. The Whimbrel took flight after about 5 m of running with its wings spread and flew south sweeping side to side making sharp turns. The raven pursued the Whimbrel for about 20–25 s into tall grass in a nearby pasture approximately 120 m from me.

I lost sight of the Whimbrel in the tall veg-

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etation, but the raven was partially visible when it lifted its head. After about 20 s, the raven hopped up to a 1 m tall fence post with what appeared to be feathers in its bill. The raven stroked its bill on the fence post 3–4 times, then jumped back down toward the Whimbrel. I heard a screech, after which I neither heard nor saw the Whimbrel again. After 30 s, the raven jumped back on the fence post, stroked its bill several times, flew 5 m landing in the grass, and hopped back to where the Whimbrel had landed. This pattern of jumping up on the fence post, flying away, landing nearby, and hopping back to the Whimbrel occurred three more times. The fourth time the raven remained at the site where the Whimbrel was last observed and was only occasionally visible. I watched for an additional 20 min but the tall grass prevented any further observations. When I left the scene at approximately 11:25, neither bird had departed.

The next day I returned to where I had last seen the birds. I noticed 100–150 Whimbrel feathers scattered in the grass, some held together by fresh blood stained cartilage. Goodwin and Gillmore (1976) stated that ravens conceal their kills, and despite the absence of a carcass, I believe the raven successfully killed the Whimbrel.

Although I did not observe the falcon attack the Whimbrel, I believe that the falcon initiated an attack and injured the Whimbrel while both were flying. I could not locate documentation of Peregrine Falcons attacking Whimbrels, although they are capable of attacking similar sized prey (Cade and Digby 1982). I speculate that the raven recognized that the Whimbrel was injured and stole the prey from the falcon. While conducting research in the Arcata Bottoms, I have observed ravens kleptoparasitizing voles (*Microtus* sp.) from White-Tailed Kites (*Elanus leucurus*) and Northern Harriers (*Circus cyaneus*). J. Dunk (pers. comm.) observed ravens position themselves on fence posts adjacent to a field in the Arcata Bottoms where Great Egrets (*Casmerodius albus*) were foraging for voles (*Microtus* sp.). The ravens were observed successfully harassing the egrets that had captured voles. These incidences show that ravens are capable of killing large prey, often sick or injured animals, but also capable of taking advantage of foraging tactics used by other species much to their own benefit.

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Wilson Bull., 112(3), 2000, pp. 431–432

Bird Behavior During a Total Solar Eclipse

Elliot J. Tramer[1]

ABSTRACT.—I report avian behavioral responses to a total solar eclipse on the north coast of Venezuela during the afternoon of 26 February 1998. Magnificent Frigate-birds (*Fregata magnificens*), Brown Pelicans (*Pelecanus occidentalis*), and Royal Terns (*Sterna maxima*), which had been foraging over the water before the eclipse, left the bay 39 (terns) or 13 (frigate-birds and pelicans) min before the eclipse became total. The frigate-birds flew inland and the pelicans went to roosts on cliffs bordering the bay. Residents of the local village, who knew the birds' behavior well, remarked that the frigate-birds and pelicans were behaving as they normally did at sunset. Laughing Gulls (*Larus atricilla*) ceased foraging and flew rapidly back and forth over the water in a tight flock during the 3 min 40 s of totality. Twelve minutes after the solar disc emerged, the frigate-birds and pelicans began to return to the bay, and they and the gulls resumed foraging. The terns still had not reappeared more than 1 hr after totality. Solar eclipses, although of brief duration, apparently reduce light levels sufficiently to temporarily interrupt normal avian diurnal behavior. *Received 16 August 1998, accepted 22 April 2000.*

The following observations of avian behavior during the solar eclipse of 26 February 1998 were made from the beach in the town of Amuay (11° 45′ N, 70° 20′ W), a small fishing village on the west coast of the Paraguaná Peninsula, Falcón State, Venezuela. At Amuay, the moon made first contact with the solar disc at 12:37 Atlantic Standard Time and totally covered the sun for a period of 3 min 40 s between 14:09 and 14:13. Last lunar contact with the sun occurred at about 15:35. The sky was cloudless during the duration of my observations.

When I arrived at the beach before 12:00, approximately 20 Magnificent Frigate-birds (*Fregata magnificens*) and 8 Royal Terns (*Sterna maxima*) hunted over the bay, and about 20 Brown Pelicans (*Pelecanus occidentalis*) and 30 Laughing Gulls (*Larus atricilla*) either fed from the bay or rested on the water. The local villagers informed me that these birds were normally present and exhibited this behavior during the winter afternoons.

The light level was noticeably dimmer about 13:30, when the sun was half-obscured. At that time I noticed that the Royal Terns were gone, although I had not noted their departure. At 13:56 the sun was 7/8 obscured and the dark shadow of the total eclipse was visible across the bay to the west. At this time, the frigate-birds ascended 75–100 m into the sky and disappeared inland. Simultaneously, the pelicans flew off in single file to their roosts on cliffs across the bay. Local villagers commented that the frigate-birds and pelicans were behaving as they normally did at sunset. The gulls, some of whom had been airborne, formed a loose flock floating on the water surface. When the pelicans and frigate-birds departed, the light levels resembled conditions just before sunset. The calculated light intensity was about 1.6×10^5 lumens/m^2 (S. Lee and A. Witt, pers. comm.).

During the total eclipse no birds were in sight except gulls, which left the water in a tightly-packed flock and flew back and forth rapidly and erratically, settling back onto the water's surface only when the edge of the solar disc reappeared from behind the lunar shadow at 14:13. During totality the light level appeared equivalent to late dusk, with the colors of objects no longer distinguishable and the brightest stars and planets clearly visible. The calculated light intensity at totality was 0.43–0.86 lumens/m^2 (D. D. Meisel, pers. comm.).

By 14:25, with the sun still more than 2/3 obscured, the pelicans and frigate-birds began returning to the bay, and the gulls resumed feeding. By 15:00 the frigate-birds and pelicans resumed feeding. The Royal Terns had not yet reappeared when I left the area at

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15:45. Their departure may not have been stimulated by the lower light intensity.

Published observations of avian behavior during a solar eclipse are apparently very few. Carmona and Amador (1995) observed increased competition for resting sites among frigate-birds in the Gulf of California during a total eclipse. Maccarone (1997) noted that four diurnal species of Ciconiiformes returned to their nesting colony in greater than expected numbers during an annular (partial) eclipse, but the noctural Black-crowned Night-heron (*Nycticorax nycticorax*) exhibited no apparent response. During a total solar eclipse in India, Trigunayat (1997) observed that roosting Black-crowned Night-herons altered a variety of behaviors, including increased calling, preening, and perch shifting. These limited observations suggest that solar eclipses, although of brief duration, reduce light levels sufficiently to temporarily interrupt normal avian diurnal behavior patterns.

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Distribution of Bacteria on Feathers of Some Eastern North American Birds

Michelle M. Muza,[1,2] Edward H. Burtt, Jr.,[3] and Jann M. Ichida[4]

ABSTRACT.—The plumage of birds harbors diverse bacteria but their distribution on feathers is unknown. We plucked a single contour feather from the venter of each of 75 passerines captured in mist nets in September, October, and November 1995. Bacteria were significantly more abundant on the distal part of the feather than the proximal part. We suggest that feathers may be a barrier to bacterial infections of the skin and that distal barbs are more likely to be damaged by feather-degrading bacteria than proximal barbs. *Received 17 Sept. 1998, accepted 22 April 2000.*

The plumage of birds provides a habitat for bacteria (Burtt and Ichida 1999) and fungi (Hubálek 1976, 1978; Pugh 1964, 1965). Among the bacteria that have been cultured from the plumage are *Bacillus licheniformis* (Burtt and Ichida 1999) and *Streptomyces* sp. (Wenger, unpubl. data), both of which degrade feathers through secretion of a keratinase enzyme (Lin et al. 1992, Böekle et al. 1995). Feathers provide insulation; the shape, lift, and propulsion necessary for flight; and a colored surface for optical signaling (Hailman 1977, Gill 1995). The effect of microorganisms on the function of the plumage may depend on their distribution on the feather but that distribution is unknown. As a first approximation to plotting the microbial distribution on the feather, we sampled proximal and distal halves of individual contour feathers from birds captured in mist nets.

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TABLE 1. Species of birds and number of individuals from which an abdominal contour feather was sampled for microorganisms in 1995.

Species	13 September	21 October	3 November
Eastern Wood-Pewee (*Contopus virens*)	1	0	0
Carolina Chickadee (*Poecile carolinensis*)	0	2	0
Tufted Titmouse (*Baeolophus bicolor*)	0	1	0
White-breasted Nuthatch (*Sitta carolinensis*)	0	1	0
Swainson's Thrush (*Catharus ustulatus*)	1	0	0
Gray Catbird (*Dumetella carolinensis*)	6	0	0
Yellow-rumped Warbler (*Dendroica coronata*)	0	1	0
Bay-breasted Warbler (*D. castanea*)	1	0	0
American Redstart (*Setophaga ruticilla*)	1	0	0
Common Yellowthroat (*Geothlypis trichas*)	2	0	0
Song Sparrow (*Melospiza melodia*)	5	1	1
Swamp Sparrow (*M. georgiana*)	0	1	0
White-throated Sparrow (*Zonotrichia albicollis*)	0	10	5
White-crowned Sparrow (*Z. leucophrys*)	0	0	2
Northern Cardinal (*Cardinalis cardinalis*)	2	3	2
House Finch (*Carpodacus mexicanus*)	0	0	3
American Goldfinch (*Carduelis tristis*)	0	3	1
House Sparrow (*Passer domesticus*)	6	2	11
Totals	25	25	25

METHODS

We placed mist nets near feeders and in net lanes cut through secondary growth at the home of E.H.B. near Ashley, Ohio (40° 26′ N, 82° 59′ W) on 13 September, 21 October, and 3 November 1995. We sampled 25 passerines in September, October, and November (Table 1). Because bacteria are more likely to occur on the venter (Burtt and Ichida 1999) than on the dorsum, wings, or tail, we removed one contour feather from midway along the right ventral feather tract of each bird. Forceps for removing the feather were sterilized in alcohol, removed just prior to use, and the residual alcohol burned off in the flame of an alcohol lamp. The feather was plucked and immediately cut into distal, pennaceous and proximal, pennaceous and plumulaceous halves using flame-sterilized scissors. As soon as the feather was cut, the distal and proximal halves were streaked across separate petri dishes four times to inoculate the nutrient agar. In each case most of the vane (about 0.25 cm^2) of the feather contacted the surface of the agar. The scissors and forceps were sterilized after each sample to prevent cross-contamination. All birds were subsequently banded and released. Recaptures were not sampled.

Our sampling technique was adapted from that recommended for sampling the surface of leaves (Langvad 1980, Donegan et al. 1991) and skin (Hambraeus et al. 1990, Bettin et al. 1994, Miller et al. 1994). Contact (Rodac) culture plates are less efficient than sampling with membrane filters but are easier to use in the field, faster, and have comparable reliability (Poletti et al. 1999). We chose nutrient agar because it is a rich medium that grows a broad spectrum of microorganisms.

The plates were placed in an incubator within 2.5 hours of sampling and were incubated at 35° C. After 12 hours of incubation colonies were just visible on the culture plates. After 36 hours, some colonies had merged and could not be counted. Therefore, we counted the total number of colonies/culture at 24 hours of incubation. Bacteria were categorized as spore-forming rods, non-spore-forming rods, and cocci based on colony morphology and a key we have developed for use on birds. A few species have sufficiently distinctive colony morphology (e.g., *B. licheniformis, B. cereus*) to be identified by species. JMP version 3.1 for MacIntosh (SAS Institute, Inc 1995) was used for calculation of two-way analysis of variance.

RESULTS

The number of bacterial colonies/culture plate in September was significantly fewer than the number in October and November ($F_{2,142} = 11.01$, $P < 0.001$; Fig. 1). More bacterial colonies were cultured from the distal half of the feather than from the proximal half ($F_{1,143} = 22.99$, $P = 0.001$; Fig. 1). The interaction of month with the distal and proximal abundance of bacteria was also significant ($F_{2,142} = 3.19$, $P = 0.044$). Types of bacteria from proximal and distal halves were similar across months, except for the absence of *B. licheniformis* in the September sample.

DISCUSSION

There were fewer colonies/culture in September and more in October and November

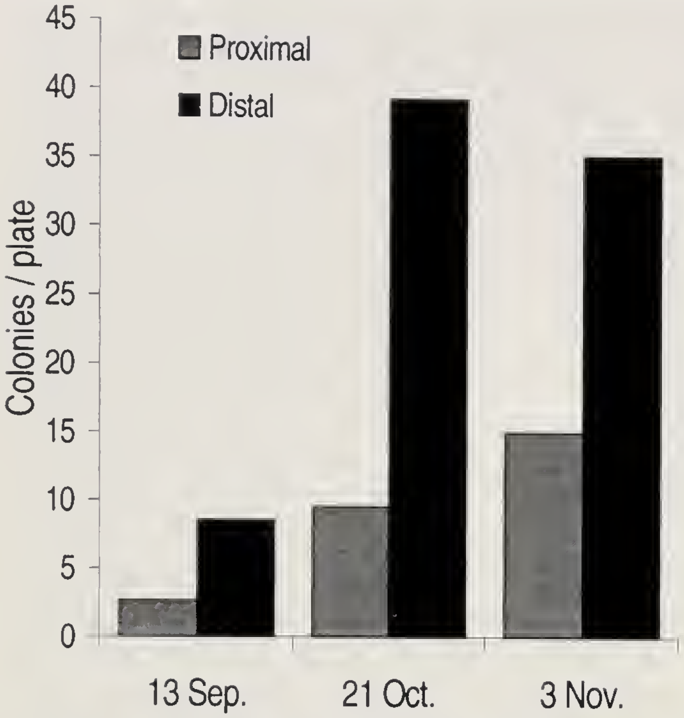

FIG. 1. The mean number of bacterial colonies per sample plate plotted by month of collection for distal and proximal halves of ventral contour feathers plucked from songbirds captured in mist nets.

for both proximal and distal portions of the feather. Burtt and Ichida (1999) found a similar pattern for *B. licheniformis,* which was scarce in September following the annual molt but recovered to premolt abundance by November.

The number of bacterial colonies/culture plate from distal portions of contour feathers exceeded the number of colonies/culture plate from proximal portions in all months in which samples were collected. Based on that difference we suggest that plumage may provide an effective barrier to infection of the skin by bacteria such as *Staphylococcus aureus,* which can cause serious skin infections (Black 1996). Furthermore, the distal concentration of bacteria suggests that vegetative cells and spores are filtered from the air or picked up through contact with the ground or vegetation and concentrated distally where conditions for bacterial growth, for example heat from the body and shielding from ultraviolet radiation, are least favorable. Most species of bacteria found on the feathers of birds are spore-forming rods [e.g., *Bacillus* species (Burtt and Ichida 1999)]. Under the harsh conditions that occur distally, these bacteria will form spores that lodge in the distal, pennaceous structure of the contour feathers that comprise the outermost surface of the body. That such spores remain viable is evidenced by their rapid growth when we remove them to appropriate culture media and incubate them at a favorable temperature. Whether the spores can develop on the feathers and whether feather-degrading species (e.g., *B. licheniformis*) harm feathers on the bird is unknown.

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Ornithological Literature

Edited by Sara R. Morris

BIRDS OF INDIA, PAKISTAN, BANGLADESH, BHUTAN, SRI LANKA, AND THE MALDIVES. By Richard Grimmett, Carol Inskipp, and Tim Inskipp. Princeton University Press, Princeton, New Jersey. 1999: 384 pp., 153 color plates, and 1270 range maps. $29.95 (paper).

A FIELD GUIDE TO THE BIRDS OF SRI LANKA. By John Harrison, illus. By Tim Worfolk. Oxford University Press, New York. 1999: 48 color plates, many range maps and several text figures. $100.00 (cloth), $60.00 (paper).

A GUIDE TO THE BIRDS OF SOUTHEAST ASIA. By Craig Robson. Princeton University Press, Princeton, New Jersey. 2000: 104 color plates, several text figures. $59.50 (cloth).—These three compact field guides now ensure that the birdwatcher and field researcher visiting South and Southeast Asia have, at their fingertips, handy and high quality fieldbooks for these two very rich avifaunas. This represents a bonanza for the bird student of the Indian Subcontinent as well as mainland Southeast Asia. Each of these three books represents a significant step forward in the art of field guide production over previous works available.

The Grimmett et al. (here termed "Grimmett") volume of South Asian birds is a much-compacted version of their bulky "guide", which appeared earlier in 1999. This is, in fact, the field book, whereas the other was a reference to keep in the car or the home—much too big to tote. This compact guide (it really is compact and field-sized) includes all the same plates and improved range maps (now with color), and facing page text. Reproduction of the reduced-size color plates is superb, and the plates as a whole are excellent. This will be an indispensable field companion for birders in region.

The Harrison guide to birds of Sri Lanka is about the same size as the preceding, but covers a tiny portion of that covered by the other two works. This new guide to Sri Lanka is a an improvement over the 1994 guide by Kotagama and Fernando, which lacks modern plates and a comprehensive text. By contrast, the Harrison guide is complete, with a nice set of modern plates and maps, and is well annotated, with facing page text and full species accounts. The species accounts include data on identification, voice, status and distribution, nesting, and range. The question is, should the reader visiting Sri Lanka purchase Harrison or simply use the Grimmett volume? The Harrison volume offers some advantages, including larger maps that focus only on Sri Lanka, and the full species accounts separate from the facing page text.

Robson's field guide to mainland Southeast Asia is a marvelous advance over the classic, but now out-of-date, Ben King guide published 25 years ago. The Robson work is fully conforming to the quality expected of a modern field guide, although it does not offer range maps. It has a slightly larger trim size than that of the Grimmett work, which will make it slightly less convenient in the field, but it is not overly bulky. The species accounts text is in a small font and is presented in a single column of text; this makes reading somewhat difficult, as does the running together of all the accounts sections into a single narrative without distinct lead headers (in contrast with the easier-to-read Harrison/Sri Lanka guide). It is clear this formatting was employed to achieve a strict economy of space. Robson has worked to keep his guide of a size suitable for the field and should be commended for this.

For me, a modern field guide must succeed, in large part, on its treatment of vocalizations. How do these three fare in this realm? The Grimmett guide to South Asia fails entirely, by including no information on vocalization. Even a bird known mainly by its voice, such as the Brown-capped Babbler (*Pellorneum fuscocapillum*) of Sri Lanka, is not characterized by this feature in the text. By contrast, the Harrison book gives a detailed and competent description of this bird's vocal repertoire. The Robson volume gives good detailed vocal accounts, as well, as evident from the text for the similarly-vocal Black-capped Babbler (*P. capistratum*). In fact, Robson's treatment of song and voice is the best of any guide available today for South/Southeast Asia. Even the unabridged version of Grimmett is not as complete (see, for instance, its description of the song of the Brown-capped Babbler).

To sum up my assessment of these books, I would posit that the Grimmett volume has the best color plates of the lot, and thus will dominate the Indian birding market. For the Sri Lanka niche, it is safe to say that the Harrison book is good enough to serve all needs. For mainland Southeast Asia, the Robson guide is excellent and detailed without being too bulky. Frankly, any field ornithologist or birder working in South and Southeast Asia will need to have all three volumes.—BRUCE M. BEEHLER.

STOPOVER ECOLOGY OF NEARCTIC-NEOTROPICAL LANDBIRD MIGRANTS: HABITAT RELATIONS AND CONSERVATION IMPLICATIONS. Edited by Frank R. Moore. Studies in Avian Biology No. 20. Cooper Ornithological Society, Camarillo, California. 2000: 133 pp. $18.00 (paper).—This volume is the result of a symposium on stopover ecology presented at the American Ornithologists' Union meeting in Missoula, Montana, in 1994. These papers range from landscape level analyses to specific studies of habitat use at local scales. Although many of the papers relate to the northern coast of the Gulf of Mexico, there are papers from Rhode Island, Virginia, and New Mexico as well as several papers that look at multiple geographic locations.

The papers are introduced in a Preface by the editor in which he places each paper in the context of migrant-habitat relationships (including intrinsic and extrinsic factors as well as differences in scale) and conservation implications. The first papers that follow are "Application of Spatial Models to the Stopover Ecology of Trans-Gulf Migrants" and "Habitat Use by Landbirds Along Nearctic-Neotropical Migration Routes: Implications for Conservation of Stopover Habitats," both of which focus on landscape scale interactions between migrants and stopover habitats. The former uses landscape-level metrics to investigate how differences in the landscape will affect the relative suitability for migrants to find appropriate stopover habitats in different energetic conditions. The second paper reviews current literature on habitat selection by landbirds during migration, which is limited. Based on species-specific habitat preferences, which often correspond better to breeding habitats than to factors such as food availability and low predation risks, the author concludes that conservation strategies for migrants need to be prepared on a species by species basis. Habitat selection is explored on a smaller scale using radio-telemetry to investigate movements of Summer Tanagers in the third article, "Mechanisms of *En Route* Habitat Selection: How Do Migrants Make Habitat Decisions During Stopover?" This study demonstrates that energetic condition appears to influence habitat exploration at stopover sites because the authors found that lean birds were more active and visited more habitats than fatter birds.

The need to investigate differences within a species, both in terms of age and sex groups and in terms of seasonal differences, are explored in "Age-Dependent Aspects of Stopover Biology of Passerine Migrants" and "Behavioral, Energetic, and Conservation Implications of Foraging Plasticity During Migration." Numerous differences in migration and stopover biology between young and adult birds including differences in fat stores, mass, stopover length, and mass change are summarized in the former, although differences are not universal and vary substantially among species. In the latter article, the consequences of dietary shifts during migration, particularly from insects to fruits in the fall, are evaluated. Such shifts, and the potential seasonal differences in habitat utilization are discussed in terms of conservation, thus continuing the themes of habitat use and conservation.

Two case studies of stopover on the northern Gulf coast and the southwestern United States follow as case studies, "Disruption and Restoration of *En Route* Habitat, a Case Study: The Chenier Plain" and "Landbird Migration in Riparian Habitats of the Middle Rio

Grande: A Case Study." An additional case study is described in "Conservation of Landbird Migrants: Addressing Local Policy" in which government (at federal, state, and local levels) and private partners jointly sponsored research on migration in Northampton County, Virginia, that is currently being used in zoning and memoranda of understanding for habitat protection. This article addresses the importance of privately owned lands as stopover habitats and illustrates the need for scientists to be involved in land-use decisions by providing information critical to policies that will benefit birds. The volume ends with a chapter that calls for additional information about and attention to migratory periods in conservation of landbirds. This chapter, "On the Importance of *En Route* Periods to the Conservation of Migratory Landbirds," briefly summarizes the importance of migratory periods in terms of species-specific patterns of geographic distribution (which may change seasonally), patterns of habitat use during migration, effects of the migratory period population regulation, and the value of migratory feats that can spur interest in migrants and thus potentially lead to support for conservation measures.

Other than a few minor editorial errors, my only real criticism of the volume is the limited number of contributions. Given the recent increase in the study of stopover biology, additional articles from several different areas of stopover biology would have provided an even stronger volume. For example, weather radars are being used to investigate the volume of migration and to determine important stopover sites. The radar work by Sidney Gauthreaux investigating locations that seem to concentrate migrants along the northern coast of the Gulf of Mexico would be a natural choice for inclusion with the selected papers. Likewise, several studies have been conducted along the Great Lakes and at inland sites in Minnesota that have proposed mechanisms for comparing the quality of stopover sites. Nonetheless, this volume contains a variety of substantial review papers, several of which include previously unpublished work, on the stopover ecology of migrant landbirds and a fantastic bibliography of works on stopover ecology. This book should be in the library of any ornithologist interested in bird migration or in conservation of landbirds and their habitats.—SARA R. MORRIS.

COLORADO BREEDING BIRD ATLAS. By Hugh E. Kingery (Ed.), line-drawing illustrations by Radeaux. Colorado Bird Atlas Partnership and Colorado Division of Wildlife. Distributed by: Colorado Wildlife Heritage Foundation, PO Box 211512, Denver, CO 80221. 1998: 636 pp., 16 pages of color photographs (mostly habitat), >1000 line-drawings, range maps, graphs, charts, and tables. $34.95 (hardcover).—This book is the product of a massive cooperative effort that included 8 field seasons (1987–1994) of work by volunteers and, during the final two seasons, paid "blockbusters." Colorado is a formidable state to atlas because of its extremes in topography (reference was made to the chauvinistic claim that if Colorado were flattened out it would be bigger than Texas), a wide range of habitat types, and many virtually inaccessible areas. The mostly volunteer work force, together with support from granting agencies and various state and federal agencies, enabled the completion of the field work, analysis and publication. The atlas project followed the North American Ornithological Atlas Committee protocol of subdividing U.S. Geological Survey topographic maps into six blocks of approximately 10 square miles (25 km^2). A "priority" block was selected for intensive coverage from each map thus targeting 1760 of 10,848 blocks in the state. Data were also collected from some non-priority blocks, especially for special habitats such as state wildlife areas; data were reported from 2769 blocks. A brief introductory chapter is followed by a chapter on atlas organization and methods that includes a detailed table of habitat codes and a section on biases and limitations (e.g., inadequate coverage of riparian habitats with high species richness and density). The magnitude of the effort is documented; 1170 field workers filed field cards, drove about 650,000 miles, and produced a final database of 86,499 bird records. Colorado had 264 species confirmed as breeding including 13 new for the state. Abundance estimates totaled over 40 million breeding pairs. A broad spectrum of analyses are reported, e.g., tables of the most abundant species, species with the highest confirmation rates, and species reported in the most blocks. Sixteen pages of color photographs highlight Colorado habitats and their breeding birds. Physiographic regions, vegetation zones, and a detailed classification of Colorado ecosystems and the birds that are part of them is provided in a chapter entitled "The Colorado Environment." Chapters on post-settlement changes and Colorado ornithologists complete the introductory material.

The bulk of the book (>500 pp.) presents species accounts. The typical species account occupies two facing pages with a map occupying slightly over half of the second page. This leaves considerable space for the species account, and they are generally thorough. They consist of sections on habitat, breeding, and distribution. A bar graph depicting the number of blocks for each habitat type from which birds were reported is included in the habitat section. The breeding section contains a table of breeding phenology. The distribution section discusses the species' distribution world-wide, and makes comparisons with Breeding Bird Survey data, and standard references to Colorado birds. The species accounts are thoroughly documented in the text, which, although it makes the accounts more difficult to read, is enormously useful to anyone wishing to learn more about a particular species. A breeding evidence table listing the number of blocks and percentage of blocks where the species was reported accompanies the map. The maps are in black-and-white, with blocks of black (confirmed), dark gray (probable), or light gray (possible) depicting breeding distribution in the state. The format is large enough that the map is easily readable and there is no difficulty separating the three shades of black to gray. The sometimes multiple line drawings are attractive, and often depict interesting behaviors. The species accounts section of the book concludes with brief accounts of species that were confirmed breeding at less than three sites, species that were reported but not confirmed, and birds that were recorded breeding before or after the atlasing period. The book concludes with appendices that list atlas block statistics, abundance estimates (conservative, "a starting point to evaluate the relative abundance of species that breed in Colorado"), a sample field card, a gazetteer, scientific names, and citations and references.

This is a thorough, attractive, and impressive book. The introductory section claims that the list of citations consists of 1338 references, many of a local nature, and as is usual for breeding bird atlases, the references alone are more than worth the price of the book. At $35 it is a remarkable bargain. Anyone interested in bird distribution will want this book.—WILLIAM E. DAVIS, JR.

ORIOLES, BLACKBIRDS & THEIR KIN. By Alexander F. Skutch. Scratchboard illustrations by Dana Gardner. University of Arizona Press, Tucson. 1996: 291 pp. $22.95 (paper).—Arguably the most diverse family of oscine passerines, the Icteridae (or Icterinae), now has two books devoted to surveys of the whole family. The first, the book under review, was followed by NEW WORLD BLACKBIRDS: THE ICTERIDS, by A. Jaramillo (author) and P. Burke (artist) published by Princeton University Press, Princeton, New Jersey (431 pp., two black and white drawings plus a page devoted to the topography of a generalized icterid, plus 39 color plates). The format of Jaramillo and Burke (hereafter J&B) resembles that of the numerous "family" books published in England by Helm. The text of the latter book is more formally arranged than is the Skutch book. Each species is allotted one or more color plates, plus paragraphs on Identification, Voice, Description, Geographic variation, Habitat, Behavior, Nesting, Distribution and Status, Movements, Molt, Measurements, Notes, and References. Skutch's text is less formal, but manages to include much of the same information, based more on personal observation than from gleaning the literature. Skutch's text is less comprehensive. A chapter entitled '"Some South American Icterids" covers 11 species not known first-hand by Skutch, hence extracted from the literature. The J&B text is more taxonomically arranged than that of the Skutch book which has discussions of major subgroups of the family (some, such as the Jamaican Blackbird, *Nesospar nigerrimus*, and the Bobolink, *Dolichonyx oryzivorus,* are single-species "groups.")

Skutch has made an error that is all too common; in the captions for the Bobolink drawings he has changed the spelling of the specific epithet from the Latin noun (*oryzivorus*) to an English adjective (*oryzivorous*). In his text he correctly states that the Baltimore (*Icterus galbula*) and Bullock's (*I. bullockii*) Orioles were lumped as the "Northern Oriole" primarily owing to their propensity to hybridize in the interior of North America where their ranges overlap. Nevertheless the figure on page 184 that is labeled "Baltimore Oriole, *Icterus galbula,* male," actually represents the so-called "Black-backed" Oriole (*I. abeillei*), which is a heavily melanized population of Bullock's Oriole (see plate 10 of J&B). On page 194, however, there is a drawing of a *bona fide* Baltimore Oriole.

J&B has a more comprehensive bibliography than Skutch, with 976 entries versus 116. A personal note may be forgiven: Skutch missed the seven papers of which I was author or co-author that are listed by J&B.

The illustrations in the Skutch book although handicapped by the lack of color give good impressions of the taxa portrayed. J&B illustrate every species, including age and sex classes where appropriate. Here the artist was handicapped, as so many of the species are simply black. Iridescence is poorly rendered (see *Quiscalus* on plates 34 and 35, *Euphagus* on plate 36, and *Molothrus aeneus* on plate 38). The "Palewing" (*Molothrus badius fringillarius*) is not pale enough. Many species are portrayed in flight, a useful feature for identification purposes. In several plates (14, 15, 28, and 30) the flying figures have what appear to be Peterson-like lines calling attention to distinctive markings, but in some of these plates this line actually represents the edge-on view of the near wing, looking deceptively like a "Peterson line." In addition to the color plates, J&B present line drawings of the distinctive Caribbean races of the Black-cowled Oriole (*Icterus dominicensis*), back patterns of male Streak-backed Orioles (*I. pustulatus*), variation in adult female Baltimore Orioles (*I. galbula*), tail patterns of male and female Audubon's Oriole (*I. graduacauda*), wing shape differences between "Bicolored" Redwings (*Agelaius phoeniceus gubernator*) and Tricolored Blackbird (*A. tricolor*), heads of female Redbreasted and White-browed Blackbirds (*Sturnella militaris* and *S. superciliaris*), face patterns of North American meadowlarks (*S. magna, S. lilianae,* and *S. neglecta*), tail patterns of yellow-breasted meadowlarks (*Sturnella* spp.), head and bill shapes of black icterids and of northern hemisphere orioles (*Icterus* spp.), and tail patterns of oropendolas (*Psarocolius* spp.).

The name of the late bird artist Louis Agassiz Fuertes seems to have given J&B trouble; on page 217 the pale form of the Orchard Oriole (*I. spurius*) is twice rendered "Fuerte's," also on page 44 where the name is rendered as *fuerteri.*

If you cannot afford to buy both books, the J&B has the advantage of completeness, whereas Skutch's discussion has the authority of personal observations, written in an easily readable style.—KENNETH C. PARKES.

CHASING WARBLERS. By Vera and Bob Thornton. University of Texas Press, Austin, Texas. 1999: 160 pp., 90 unnumbered color photographs, 1 map. $40.00 (cloth), $19.95 (paper).—This book chronicles the authors' quest to photograph the 52 species of warblers (family Parulidae) that breed in the United States, a quest that spanned ten years. The book is organized in chapters that correspond to the authors' trips to photograph all of the species. Birders will enjoy the accounts of numerous fallout sites that are often visited by birders during migration including High Island, Texas, and Point Pelee, Ontario. Although a number of photographs were taken at migratory stopover sites including the Dry Tortugas and Crane Creek in Ohio, a number of the locations were within the breeding range of the species. For example, pictures of the Kirtland's Warbler (*Dendroica kirtlandii*) come from Mio, Michigan, and pictures of several species of warblers were taken in the mountains of Arizona and West Virginia.

The photographs in this book are beautiful. Most are of males in their alternate plumage during spring migration or the breeding season. In the first chapter, the authors describe their photographic equipment, film, and philosophy. In particular, their quest involved photographing the brightest, most colorful individuals in as natural a setting possible, rather than attempting more "textbook-clinical" shots. Most species are represented by several photographs, often from different locations, and showing some of the variation among individuals.

The authors include natural history information about many of the species. For example, interspersed among the description of photographic locations is information about the general annual cycle and the migration of warblers across the Gulf of Mexico. The authors describe the nests they encountered of several of the species including their first Ovenbird (*Seiurus aurocapillus*) nest encountered during their trip to West Virginia. Additional information can be gleaned from the descriptions of the preferred habitats of species and the wintering habits of species including the discussion of the difficulty of photographing the Northern Waterthrush (*S. noveboracensis*) in Belize.

I was somewhat disappointed by the authors' decision to only show the colorful male plumage, ignoring the subtle beauty of the females, many of which are stunning and are regularly overlooked. Additionally, the authors chose not to include pictures of birds at the nest although they describe several photographs taken that they did not include. Nonetheless, warbler enthusiasts will enjoy the colorful pictures and birders may enjoy the descriptions of so many of the birding hotspots.—SARA R. MORRIS.

A BIRDER'S GUIDE TO THE RIO GRANDE VALLEY. By Mark W. Lockwood, William B. McKinney, James N. Paton, and Barry R. Zimmer. American Birding Association, Inc., Colorado Springs, Colorado. 1999: 280 pp. Black and white photos, 40 maps. $23.95 (wire-O binding).—This is the third revision of the publication by this name and the second produced and printed by the American Birding Association (ABA). This guide follows the standard ABA bird finding guide format with useful thumbnail maps, site descriptions, and specific information on finding birds in the region.

The authors have chosen to provide an annotated checklist instead of bar graphs to describe the status and distribution of each species due to the broad geographic area covered by this guide. The annotated checklist is useful in that it highlights the best areas to look for localized species. The checklist also includes identification information for Tropical and Couch's kingbirds (*Tyrannus melancholicus, T. couchii*) and yellowthroats. Oddly, a section on the status of montane invaders appears between Brown Creeper (*Certhia americana*) and Cactus Wren (*Campylorhynchus brunneicapillus*). This information could have been better conveyed within each species account or the Trans-Pecos section, but seems oddly out of place in its present location.

The coverage includes southern and western Texas, with *A Birder's Guide to the Texas Coast* covering areas to the north and east. Major sections of the guide include the sparsely populated Trans-Pecos, the Lower Rio Grande Valley, and the Edwards Plateau, each distinctly different in avifauna and habitat. Although the majority of the sites described are in Texas, the Trans-Pecos section also covers adjacent New Mexico including Carlsbad Caverns National Park and Las Cruces National Monument. Throughout, the guide stresses the importance of respecting private property. It provides information on access to areas open to the public, which is very useful in areas where much of the land is in private hands and closed to the public, e.g., the Davis Mountains.

Lists of butterflies and higher vertebrates of the region are also included. This book is recommended to birders visiting the area.—MARY GUSTAFSON.

NATIONAL AUDUBON SOCIETY BIRDER'S HANDBOOK. By Stephan W. Kress. Dorling Kindersley Limited, London. 2000: 163 pp., numerous unnumbered color photographs, seven unnumbered maps. $24.95 (cloth).—Bird enthusiasts range from the causal observer, to the regular bird feeders, to the birders who keep lists of every bird they see on every trip, to the more avid enthusiast who records birds with photographs and with sound recordings. This volume provides information that will be valuable to all but the most seasoned veteran bird watchers. The book is divided into six chapters entitled "Birding Techniques," "Binoculars and Scopes," "Observing Birds," "Photographing and Recording Birds," "Bird Families of North America," and "Birding Hotspots." Appendices include information about birding ethics, additional sources of information ranging from the library to the internet, sources for birding supplies, educational and research programs, and the National Audubon Society Mission Statement.

"Identifying Birds" includes tips on things to look for when encountering a bird for the first time including shape, size, behavior, posture, color, field marks, and song. Additional information about where to find birds, how to get closer, locating birds, and leading bird walks is also included. This section will be most useful to beginning bird watchers or to trip leaders who may find this information useful in teaching beginners. My major criticism is that Kress included the use of pishing, tapes, and lures to make birds more accessible but included only a relatively minor disclaimer about disturbance after the section on tapes. Given the likelihood of many beginners using this book, I would have appreciated a disclaimer at the beginning of this section and a longer explanation of the likely impact of interfering with birds, particularly on the breeding grounds, at migratory stopover sites, and at birding hotspots.

"Binoculars and Scopes" provides extensive information about comparing, purchasing, and using binoculars and spotting scopes. Kress covers various topics including how binoculars work, checking alignment, focusing binoculars, and binocular care. Less information is provided on telescopes. Similarly, "Photographing and Recording Birds" covers the information on the types of equipment available, advantages and disadvantages of different equipment, and tips to make the most of your opportunities. I was impressed with the section on filing bird slides and presenting a slide program, recommending that anyone taking the time to make pictures also share them with others. Many professionals could benefit from some of the tips on presentations. Advance birders may use this chapter to explore new ways of enjoying birds and sharing their passion with others.

"Bird Families of North America" provides tips on the identification of families rather than species. Photographs and drawings of silhouettes illustrate a brief text describing each family. The text provides some general characteristics that may help with identification and the number of species in the world and in North America. This chapter will be useful for beginners, for birders learning a new group of birds or birds in a new area, as well as teachers.

The final chapter and appendices provide additional resources relating to learning more about birds. "Birding Hot Spots" provides more than 75 areas that are generally well known for birds from every geographic area of North America. Additional information is provided in the "Bird Finding" section of Appendix 2. I was pleased to see appendices that cover building a library and information on bird related organizations and publications. Space limitations necessitated a brief coverage of many topics, so readers should be aware that many good references are not included. For example, *Birds of North America* by Robbins, Bruun, and Zim was not included among the field guides although it is the preferred field guide for many ornithologists and bird watchers. Likewise the section on birds on the internet is only two pages, with a limited number of web sites. Nonetheless, I believe that Kress has chosen his limited items well, so that most of the major books, organizations, etc. are included.

Although this volume will not appeal to many ornithologists, it will be of great benefit in the library of anyone who teaches about birds or who is in regular contact with the general public and may need a general book to recommend for someone to learn more about bird watching and birds in general. Overall, it is highly recommended.—SARA R. MORRIS.

Woodpeckers Working Group of the German Ornithologists Society (DO-G) 2001 International Annual Symposium

The German Ornithologists Society's Woodpeckers Working Group 2001 International Annual Symposium will emphasize woodpecker ecology and practical approaches in conservation strategies. The purpose of this symposium is to bring together researchers, conservation biologists, ecologists, resource managers, and environmentalists to develop better understanding and conservation management of woodpeckers. Official language is English, but German also will be accepted.

Participants are encouraged to submit a preliminary abstract on any aspect of their work on the woodpeckers. Deadline: 30 November 2000. Notice of acceptance will be sent by 15 December 2000. Accepted papers will be scheduled for 15–30 minutes oral presentation depending on number of submissions. Papers will be published in symposium proceedings.

For more information, contact: Dr. Peter Pechacek, Nationalparkverwaltung, 83471 Berchtesgaden, Germany; ++49 8657 9885913; Fax ++49 8652 968640; Email: Pechacek@t-online.de

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THE WILSON BULLETIN

SUGGESTIONS TO AUTHORS

See Wilson Bulletin, 110:152–154, 1998 for more detailed "Instructions to Authors."

http://www.ummz.lsa.umich.edu/birds/wilsonbull.html

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THE WILSON ORNITHOLOGICAL SOCIETY

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Jim Rodovich · 2000 -

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A NEW SPECIES OF SAGE-GROUSE (PHASIANIDAE: *CENTROCERCUS*) FROM SOUTHWESTERN COLORADO

JESSICA R. YOUNG,[1,7] CLAIT E. BRAUN,[2,6] SARA J. OYLER-McCANCE,[3,4]
JERRY W. HUPP,[5] AND TOM W. QUINN[4]

ABSTRACT.—The Gunnison Sage-Grouse (*Centrocercus minimus*) is described as a new species from southwestern Colorado and contrasted with the Sage-Grouse (*Centrocercus urophasianus*) from northern Colorado and western North America. Gunnison Sage-Grouse differ from all other described sage-grouse (*C. u. urophasianus, C. u. phaios*) in morphological measurements, plumage, courtship display, and genetics. The species currently is limited to 8 isolated populations in southwestern Colorado and adjacent San Juan County, Utah. Total estimated spring breeding population is fewer than 5000 individuals with the largest population (<3000) in the Gunnison Basin (Gunnison and Saguache counties), Colorado. *Received 3 February 2000, accepted 29 June 2000.*

Sage-Grouse (*Centrocercus urophasianus*; Phasianidae; Tetraoninae) occur only in North America, and historically occupied suitable shrub-steppe habitats from eastern California, Oregon, Washington, and southeastern British Columbia east into western North Dakota, South Dakota, northwestern Nebraska, southwestern Kansas, and adjacent Oklahoma (Aldrich and Duvall 1955, Aldrich 1963, Johnsgard 1973). The former distribution included portions of 16 states and 3 Canadian provinces. These grouse have been extirpated from 5 states (Arizona, Kansas, Nebraska, New Mexico, Oklahoma) and 1 province (British Columbia; Braun 1998).

Two races of sage-grouse have been described previously. *Centrocercus urophasianus phaios* is restricted to the area immediately east of the Cascade Mountains in Oregon, north into Washington and south into extreme northeastern California (Aldrich 1946). *Centrocercus urophasianus urophasianus* was reported to occur throughout the remainder of the range (Aldrich and Duvall 1955, American Ornithologists' Union 1957, Aldrich 1963).

Management activities by the Colorado Division of Wildlife to increase the knowledge about sage-grouse within the state resulted in systematic collection of wings from hunter harvest throughout the state starting in the mid-1970s. In 1977, wings from birds in the Gunnison Basin (Gunnison and Saguache counties) were noted to be smaller (based on measurements of primaries 10, 9, and 1) than wings obtained elsewhere in the state. Subsequent studies of grouse in the Gunnison Basin in the mid-1980s (Hupp 1987) and early 1990s (Young 1994) revealed significant differences in morphometrics (Hupp and Braun 1991), breeding behavior, and plumage (Young et al. 1994) compared to other populations of sage-grouse. Recent studies of the mitochondrial and nuclear allele frequencies of sage-grouse in Colorado have revealed additional significant differences (Kahn et al. 1999, Oyler-McCance et al. 1999).

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FRONTISPIECE. Male Gunnison Sage-Grouse displaying, Gunnison Basin, Colorado. Original artwork painted from life by Don Radovich.

Based on published and unpublished information on morphometrics, plumage appearance, behavior, and genetics, we propose that the sage-grouse first described from the Gunnison Basin, Colorado by Braun and Young (1995), be recognized as a new taxon. It fulfills the criteria for species distinction by several common species concepts including the biological species concept, the recognition concept, and the evolutionary species concept. Further, we propose that all other sage-grouse continue to be named with the English name Sage-Grouse. Our recommendation is not in agreement with the AOU Checklist Committee (2000), which recommends all other sage-grouse be named Greater Sage-Grouse. Internationally, nationally, and regionally the common name for the latter species for the past 5 years has been Northern Sage Grouse based on the relative locality from which it was first described. Following this point in the manuscript, the common name Sage-Grouse is used to refer to the species which has been previously described in the scientific literature and in professional abstracts as Northern Sage-Grouse or Sage Grouse.

GUNNISON SAGE-GROUSE, *CENTROCERCUS MINIMUS* NEW SPECIES

Holotype.—Denver Museum of Natural History (DMNH) 40722, adult (2+ years of age) male obtained by C.E.B. and J.R.Y. on 10 May 1993 approximately 23 km southeast of Gunnison, Gunnison County, Colorado. This locality is in the South Parlin area on public land administered by the Bureau of Land Management (BLM). This bird was prepared as a flat skin with skeleton. DMNH 40723 was collected on the same date and at the same location, also an adult male prepared as a flat skin with skeleton.

Diagnosis.—A dark brown sage-grouse with black underparts and prominent black, long, thin, specialized, ornamental contour feathers arising from the dorsal base and sides of the neck on males (lost after breeding with few apparent until molting in mid- to late November), coarsely barred brown, long tail feathers with prominent white to yellow-white bars, brown rounded wings, and feathered gray-brown tarsi. Rounded air sacs (cervical apteria) greenish-yellow within a white upper breast, with scale-like feathers on males prominent in spring. Females smaller than males, similar in general plumage appearance but without specialized ornamental contour feathers arising from the dorsal base of the neck and without the prominent white upper breast and discernible air sacs of males. Tail length shorter than males but with same coarsely barred brown with prominent white to yellow-white bars. Both sexes smaller in mass and feather lengths than adult/yearling *C. urophasianus* with no overlap. Strut rates are slower and audible sounds differ markedly from *C. urophasianus* during breeding displays.

Distribution.—Gunnison Sage-Grouse currently exist in 6, possibly 7, counties in southwestern Colorado (Braun 1995, Commons 1997) and 1 county in southeastern Utah (Barber 1991). The known historic distribution (Fig. 1) of this species in Colorado was in sagebrush (*Artemisia* spp.) communities below 3000 m south of the Eagle and Colorado rivers from near Leadville (Lake County) south, and in sagebrush dominated shrub-steppe habitat into the San Luis Valley to the boundary with New Mexico and west to the Utah state line. It was known to occur in Grand and San Juan counties, Utah, south and east of the Colorado River. The distribution of the species was discontinuous within this area (Rogers 1964, Braun 1995) separated by river valleys and high forested mountains.

We hypothesize that sage-grouse formerly native to New Mexico (Bailey 1928, Merrill 1967, Hubbard 1970) belong to this species. This would exclude those trapped in Wyoming and released at a number of locations to supplement sage-grouse populations historically present in the northern areas of the state (Merrill 1967). We found no museum specimens from New Mexico (J. P. Hubbard, pers. comm.), Arizona (Phillips et al. 1983), Kansas (Goss 1883, Cable et al.1996), or Oklahoma (Nice and Nice 1924, Sutton 1967) to test the general hypothesis that sage-grouse in all of these locations were Gunnison Sage-Grouse. The areas in northern New Mexico and extreme northeastern Arizona once had sagebrush habitats that were mostly contiguous with areas in Colorado and Utah presently occupied by Gunnison Sage-Grouse. The identity of the sage-grouse known to have oc-

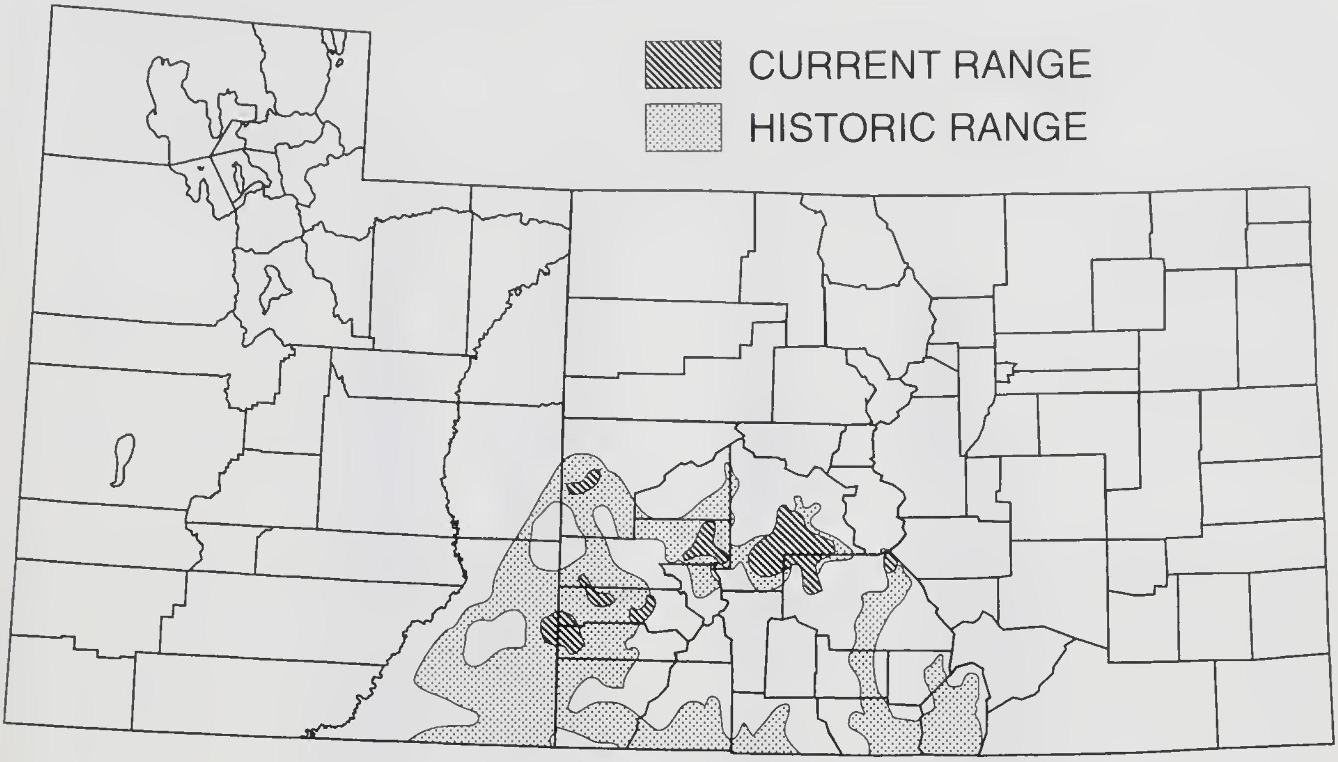

FIG. 1. Current and historic distribution of Gunnison Sage-Grouse in Colorado and Utah.

curred in extreme southwestern Kansas and adjacent northwestern Oklahoma is unknown but we postulate that they too were Gunnison Sage-Grouse because of their proximity to the current range of the species.

MORPHOMETRICS

Body mass.—Mean live body mass of Gunnison Sage-Grouse captured during the breeding season (late March–late May) was 27–33% less than mean live body mass reported by Beck and Braun (1978) for Sage-Grouse in northern Colorado (Jackson County) during April–May (Table 1). Live body mass of Sage-Grouse in Jackson County, Colorado was similar to that reported for Sage-Grouse (*including C. u. urophasianus* and *C. u. phaios*) throughout the rest of its range (Beck and Braun 1978). Differences in body mass between large and small bodied sage-grouse were greatest for males (32–33%, ca 1000 g) and slightly smaller for females (27–30%, 400–500 g; Table 1).

Length of primaries.—Fully replaced primary feathers 10, 9, and 1 were measured in place by inserting a flexible ruler between primaries 10 and 9, 9 and 8, and 2 and 1 and recording the length from the feather insertion to the tip of the primary. Wings were available from sage-grouse harvested by hunters during September hunting seasons in the Gunnison Basin and in Jackson County, Colorado. Mean

TABLE 1. Live body mass (g) of Gunnison Sage-Grouse and Sage-Grouse from Colorado during the breeding season.

	Adult males	Yearling males	Adult females	Yearling females
Gunnison				
Mean (Sample size)	2141 (89)	1911 (21)	1204 (18)	1131 (20)
Standard error	12.6	32.7	16.3	19.4
Range	1727–2435	1622–2176	1072–1327	990–1335
Jackson County[a]				
Mean (Sample size)	3190 (465)	2809 (445)	1745 (221)	1551 (186)
Standard error	8.5	9.7	10.2	9.0
Range	None given			

[a] Data from Beck and Braun (1978).

TABLE 2. Length (mm) of primary flight feathers (P10, P9, and P1) of Gunnison Sage-Grouse and Sage-Grouse in Colorado in September.

	Adult males			Adult females		
	P10	P9	P1	P10	P9	P1
Gunnison						
Mean (Sample size)	166 (79)	216 (74)	151 (78)	139 (120)	182 (131)	130 (128)
Standard error	0.43	0.55	0.30	0.54	0.32	0.32
Range	158–179	203–226	144–159	128–155	169–196	120–138
Jackson County						
Mean (Sample size)	179 (65)	230 (54)	167 (67)	147 (100)	193 (100)	141 (100)
Standard error	0.59	0.79	0.51	0.39	0.54	0.45
Range	167–190	214–240	151–176	139–157	179–210	130–151

lengths of primaries were 8–16 mm shorter for Gunnison Sage-Grouse when compared to large bodied birds (Table 2). Differences were greater for males (6–11%) than females (5–8%). Primary lengths of Sage-Grouse in Jackson County, Colorado are similar to those of Sage-Grouse in California, Nevada, Oregon (*including C. u. urophasianus* and *C. u. phaios*), Utah, and Wyoming (C. E. Braun, unpubl. data).

Beak size.—Although sample sizes from all known museum specimens are small, three standard measures indicate that adult Gunnison Sage-Grouse from southwestern Colorado have shorter and narrower beaks than Sage-Grouse from northern Colorado (Table 3). Hupp and Braun (1991) found similar differences in a larger sample of culmen lengths between Gunnison Sage-Grouse and Sage-Grouse in Jackson County.

Tail length.—Length of tail feathers of males [$\bar{x}$ = 347 ± 0.5 (SE), n = 36] is longer in Gunnison Sage-Grouse than in other Sage-Grouse (generally <315 mm), although this character is easily altered by wear. Both sexes of Gunnison Sage-Grouse have clearly defined white or cream bars (width = 5–7 mm) on the rectrices, unlike the indistinct barring on the tail feathers of other Sage-Grouse (Fig. 2). Thus, the elaborate neck feathers of males and the uniquely barred rectrices are the best field identification characters for the Gunnison Sage-Grouse.

TABLE 3. Mean beak measures (mm) of museum[a] specimens from Gunnison Sage-Grouse and Sage-Grouse in Colorado. Sample size in parentheses.

	Adult male		Adult female	
	Gunnison	Northern Colorado	Gunnison	Northern Colorado
Culmen	31.7 (3)	39.1 (4)	28.0 (4)	30.6 (9)
Nostril to tip	14.3 (3)	16.6 (4)	12.9 (4)	14.5 (9)
Width	16.0 (3)	21.7 (4)	13.8 (4)	17.1 (9)

[a] Sample sizes of museum specimens of adult Sage-Grouse from Colorado are small.

PLUMAGE

Outside the breeding season, sage-grouse throughout western North America are similar in appearance. Overall coloration varies from gray-brown to darker brown within a population and changes seasonally because of feather fading resulting from exposure to the environment and molt replacement of body feathers (C. E. Braun, pers. obs.). Sage-grouse in southwestern Colorado and southeast Utah differ from all other studied populations in length and thickness of modified feathers on the dorsal surface of the back and sides of the neck of males during the breeding season (Fig. 3). The elaborate long, thin black specialized ornamental contour body feathers that arise from the dorsal base of the neck of Gunnison Sage-Grouse adult males (range 120–173 mm, $\bar{x}$ = 146 ± 0.2, n = 38) and 3–6 mm wide give an appearance of a black "ponytail" when displayed. In contrast, Sage-Grouse have shorter and thinner (generally <115 mm long and 1 mm wide) dorsal neck feathers.

BEHAVIOR

Gunnison Sage-Grouse are similar to Sage-Grouse in that they have a lek mating system. Breeding behavior is initiated in early spring (generally in March) and terminates in late May. Many of the attributes that distinguish

FIG. 2. Rectrices of Gunnison Sage-Grouse (b and d) and Sage-Grouse (a and c). Drawn from life by D. L. Rieden.

male Gunnison Sage-Grouse from Sage-Grouse males are sexually dimorphic traits used during mating displays on the lek (Young et al. 1994). Gunnison Sage-Grouse perform their courtship displays at slower rates (Young et al. 1994). They possess a different mating call in which they pop their air sacs nine times instead of twice as does the Sage-Grouse (Young et al. 1994). Previous studies of sage-grouse indicate that some acoustical aspects of the mating display influence male mating success (Gibson and Bradbury 1985, Gibson et al. 1991). On average, only 10–15% of the adult males breed on the lek each season (J. R. Young, pers. obs.). Yearling and adult females breed; yearling males probably breed rarely.

Male courtship calls of Gunnison Sage-Grouse have been described by Young and coworkers (1994), and recordings of males and females have been deposited with the Library of Natural Sounds (LNS) at the Cornell Laboratory of Ornithology. In general, male Gunnison Sage-Grouse have mating vocalizations that are similar in duration, but different in structure from male mating vocalizations of Sage-Grouse. Gunnison Sage-Grouse females produce a variety of vocalizations on the lek; however, they have not been compared with vocalizations from female Sage-Grouse. Both male and female Gunnison Sage-Grouse vocalize off the lek and in contexts similar to those noted in the other species (J. R. Young, pers. obs.). No vocalization recordings have been obtained for either sex off the lek.

Young (1994) found that females in the Gunnison Basin and northern Colorado avoided playbacks of male courtship vocalizations that differed from the vocalizations of their local population. She concluded that differences in male courtship vocalizations were likely a barrier to mating between Gunnison

FIG. 3. Lateral views of head and neck of Gunnison Sage-Grouse (lower) and Sage-Grouse (upper). Drawn from life and photos by D. L. Rieden.

Sage-Grouse and Sage-Grouse. Thus, Gunnison Sage-Grouse appear to be reproductively isolated based on male courtship vocalizations, which act as pre-mating isolating mechanisms. Divergence of mating behaviors coupled with geographical isolation may result in the rapid evolution of a new species through sexual selection (Lande 1981, Kaneshiro and Boake 1987).

GENETICS

Sequence information from 141 bp of region I of the rapidly evolving mitochondrial control region was gathered from 201 individuals of 5 Sage-Grouse and 4 Gunnison Sage-Grouse populations within Colorado (Kahn et al. 1999, Oyler-McCance et al. 1999). Sage-grouse in general were found to have four dominant haplotypes in all populations, only one of which was found in the Gunnison Sage-Grouse populations. The Gunnison Sage-Grouse populations had one haplotype that was unique. A similar distinction between Gunnison Sage-Grouse and Sage-Grouse was found using 4 nuclear microsatellites (Oyler-McCance et al. 1999).

Both mitochondrial and nuclear markers revealed there were no significant differences among the Sage-Grouse populations indicating gene flow among them. Within the Gunnison Sage-Grouse populations, however, most pairwise comparisons with other populations showed significant differences among populations suggesting there is some population differentiation, probably as a result of their small population sizes and isolation (Oyler-McCance et al. 1999).

Thus, DNA sequence information from the mitochondrial and nuclear genomes supports the hypothesis that there is a barrier to gene flow between Gunnison Sage-Grouse and Sage-Grouse populations. This implication is made on the basis of two observations. First, there are frequency differences of shared mitochondrial haplotypes and shared microsatellite alleles between Sage-Grouse and Gunnison Sage-Grouse. Second, there are 3 microsatellite alleles and 1 mitochondrial haplotype that have remained unique to the small-bodied populations, based on the current sampling numbers.

We suggest these genetic differences are the result of reproductive isolation that is reinforced by (at minimum) the behavioral isolating mechanisms discussed previously. Hence, we conclude these are separate species according to the biological species concept. However, there are no fixed sequence differences between the two taxa so that based on the molecular data alone, an interpretation that these are species according to the phylogenetic species concept is obviated. The molecular differences we observed between these taxa are among the smallest observed for most vertebrates (Avise and Walker, 1999). Avise and Walker (1999) suggested that genealogical (phylogenetic) and reproductive traits are intimately intertwined, as are the related biological and phylogenetic species concepts. It appears the Gunnison Sage-Grouse provides an example of an intermediate stage of speciation where reproductive isolation is in place, but other molecular differences continue to diverge. Such a situation can be expected when morphological or behavioral change occur rapidly relative to changes in alternate haplotypes/alleles that are not related to reproductive isolation. Based on the extreme sexual dimorphism and the small number of males that obtain most of the matings (Wiley 1973, Vehrencamp et al. 1989), sexual selection is likely the predominant selective force.

HABITAT AND CONSERVATION STATUS

Habitat.—Nesting, brood-rearing, and summer habitats used by Gunnison Sage-Grouse have been described by Young (1994) and Commons (1997). Nesting success is highest in areas where forb and grass covers are found below a sagebrush (15–30%) canopy (Young 1994). Average clutch size (n = 24) is 6.8 (± 0.7) eggs and eggs average 54.5 (± 1.4) mm long × 38.0 (± 0.7) mm diameter. Clutch and egg sizes are within the range reported for Sage-Grouse (Schroeder et al. 1999). In winter Gunnison Sage-Grouse are restricted to areas with substantial cover (15–30%) of big sagebrush (*A. tridentata vaseyana, A. t. wyomingensis*), black sagebrush (*A. nova*), and low sagebrush (*A. arbuscula*) intermixed with native grasses and forbs and associated riparian habitats (Hupp and Braun 1989). Their winter habitat differs from Sage-Grouse; they use areas with more deciduous shrubs such as Gambel oak (*Quercus gambelii*) and serviceberry (*Amelanchier*) as well as areas invaded by piñon (*Pinus*) and juniper (*Juniperus*) at elevations of 1800–2800 m. Sagebrush leaves are probably the principle food from November into April, whereas forbs and insects are commonly eaten in summer. In disturbed and fragmented habitats, Gunnison Sage-Grouse forage and roost in cultivated fields of alfalfa, wheat, and beans (Young 1994, Commons 1997). Detailed analyses of their diet across seasons have not been done.

Conservation status.—The historic abundance is unknown but we estimate that it was several orders of magnitude larger than at present based on historical documents and interviews. Eight populations are known, totaling fewer than 5000 breeding birds of which fewer than 3000 occur in the Gunnison Basin, Colorado. Some populations are small, fewer than 150 breeding birds and several former populations are known to have become extirpated since 1980 (Braun 1995). Fewer than 150 Gunnison Sage-Grouse are known to occur in Utah. Gunnison Sage-Grouse are at risk of extinction because of habitat loss, fragmentation, and degradation (Braun 1998, Oyler-McCance 1999). In the Gunnison Basin, the average number of males attending leks has declined by more than 60% since 1953 (J. R. Young, unpubl. data). All eight small populations have high potential for inbreeding and populations that have been examined have low genetic diversity in the nuclear and mtDNA genomes (Young 1994, Kahn et al. 1999, Oyler-McCance et al. 1999). A petition has been submitted requesting listing under the federal Endangered Species Act of 1973. The Colorado Division of Wildlife, Bureau of Land Management, and other agencies within the U.S. Department of Interior, working with local agencies, interest groups, and private citizens, have developed locally derived and supported conservation plans. Some aspects of those plans are being implemented for six populations in Colorado. A conservation plan is under development for Gunnison Sage-Grouse in San Juan County, Utah, and plans are being finalized for two of the three populations in Colorado that lack approved plans. Submission of this manuscript was deliberately delayed for several years to allow completion and implementation of conservation plans to help protect the new species. With completion and implementation of useful conservation plans, it is our hope that Gunnison Sage-Grouse will continue to exist for the foreseeable future.

ETYMOLOGY

This new species is named *Centrocercus minimus* because of its relatively small size. The English name, Gunnison Sage-Grouse, is derived from the general area (Gunnison Basin, Gunnison County, Colorado) where the species was first recognized as being different and intensively studied, and in recognition of the effort by the local citizens who seek to promote its conservation.

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KILLDEER PARASITIZES MOUNTAIN PLOVER NEST

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ABSTRACT.—We discovered a Killdeer (*Charadrius vociferus*) incubating a nest containing three Mountain Plover (*Charadrius montanus*) eggs and three Killdeer eggs. The nest had been incubated about two weeks when discovered and was depredated three days later. To our knowledge this is the first known occurrence of a nest having eggs from both species. *Received 15 February 2000, accepted 23 May 2000.*

In Colorado most Mountain Plovers (*Charandrius montanus*) breed in the eastern part of the state (Kuenning and Kingery 1998). Primary breeding habitat is described as short vegetation dominated by buffalo grass (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*) on flat topography (Graul 1975, Knopf and Miller 1994, Knopf and Rupert 1999). Mountain Plovers are attracted to burned areas for nesting, feeding, and raising young (Knopf 1996). Unlike most plovers, they seek areas of local aridity and are rarely found near water (Knopf 1996). Nest sites consist of bare ground (Knopf and Miller 1994) in grazed areas, overgrazed tallgrass prairie (Luan 1957), and fallow and plowed fields on fragmented prairie (Shackford 1991, Kuenning and Kingery 1998, Knopf and Rupert 1999). Mountain Plovers begin laying eggs in late April and incubate an average of 29 days (Graul 1975). They may renest if nests are destroyed. There may be two clutches per pair; the male incubates one and the second is cared for by the female.

The Killdeer (*Charadrius vociferus*) nests statewide in Colorado and can use patches of open habitat that are too small to be used by Mountain Plovers. Killdeer breed in a variety of habitats including wet areas, dry grasslands, and gravel roads, and are often associated with wildlife or livestock (Nelson 1998). Typically, nests are on a raised area of barren ground with sparse cover. Killdeer nest as early as April and adults share in parental duties of a single nest. Eggs hatch an average of 25 days after incubation begins (Johnsgard 1981).

On 10 March 1999, three pastures were burned on Comanche National Grassland (37° 20' N, 102° 30' W), Baca Co., Colorado, to provide habitat for migrating and nesting Mountain Plovers (Svingen and Giesen 1999). Most plover nests (33 of 45) located on the Comanche in 1999 were found in one pasture (13D; 210 ha). Approximately 145 ha of the pasture were burned of which 65 ha are a quarter section. This quarter section contained 15 of 33 plover nests found within the pasture. Only three to four pairs of Killdeer were observed in the same pasture; one near the northwest corner of the quarter section, one or two near a stock tank (southwest corner), and one near the parasitized nest (southeast corner). A Killdeer was observed feigning injury previouly in the southeast corner but we did not locate a nest. Dominant vegetation was buffalo grass and blue grama.

We use the term "parasitize" to mean conditional parasitism (Amat 1998), which may occur when a female loses her partial clutch and deposits the remainder of her eggs in the nest of another individual. A parasitized nest was discovered about 750 m east of the stock tank on 18 May at 16:15 (MST) after a Killdeer was flushed from the site. The parasitized nest contained three Mountain Plover eggs (olive colored) arranged in the typical triangular pattern and three Killdeer eggs (creme colored; Fig. 1). Two eggs of each species were floated to determine status of development and all appeared to have been incubated about two weeks [i.e., egg floated vertically bobbing just above the water surface (Alberico 1995)]. When the nest was checked again 21 May at 06:32 it had been depredated. Large and small eggshell fragments of both species were found within 10 m of the nest. No Killdeer was observed near the site after the nest had been destroyed.

A number of possible events may have occurred in the combined Mountain Plover-Kill-

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FIG. 1. Eggs in the parasitized nest. Mountain Plover eggs are those in the center, upper left, and upper center. Killdeer eggs are at far right, lower right, and lower left.

deer nest. We suspect that a Mountain Plover initiated the nest and was first to lay eggs; and the Killdeer later parasitized the nest and remained to incubate, possibly after loss of its own nest. We base this speculation on four observations.

First, Killdeer nests are typically lined with pebbles or small stones (5–10 mm diameter) and have nest material such as twigs, seeds, weeds, and small plant stems (Johnsgard 1981, Nelson 1998). Nest material of the combined nest included dried manure chips, lichen, rabbit pellets, rootlets, and grass. This material is characteristic of the Mountain Plover (Knopf 1996) and was identical to other plover nests we observed.

Second, the Killdeer almost always has a clutch of four eggs (Bent 1929, Harrison 1978, Johnsgard 1981, Nelson 1998). Mountain Plover clutches typically contain three eggs although six-egg clutches have been reported (Dinsmore and Knopf 1999). It is possible that having six eggs in the nest caused the Killdeer to suppress laying its fourth. This would support the claim that the Killdeer was the second occupant of the nest. Two other possibilities exist for the nest having three instead of four Killdeer eggs. The Killdeer's first egg could have been destroyed at its own nest forcing it to find another site to complete its clutch, namely the Mountain Plover nest; a predator (e.g., canid or snake) could have removed a Killdeer egg intact from the nest before we discovered it and, within the next three days, another predator could have destroyed the remaining eggs. We suspect this latter predator was a small mammal or corvid because shell fragments were nearby.

Also, the overlap of suitable habitat in this area for both species might result in competition for territories and nest sites. Mountain Plovers are rarely seen with Killdeer (Knopf 1997), but Killdeer use diverse habitats that include plover breeding habitats, such as heavily grazed pastures, newly plowed fields, agricultural lands, disturbed areas, fallow fields (Bailey and Niedrach 1965, Nelson 1998), and especially burned shortgrass prairie (Knopf 1996). On several occasions we observed Killdeer and Mountain Plovers close together in the same fallow fields and burned pastures. The habitat around the nest seemed especially suitable for Mountain Plovers, as indicated by their high density (15 nests in 63 ha). Only three to four pairs of Killdeer were ever sighted in the pasture. Thus, it is more likely that a Mountain Plover initiated the combined nest because of the greater density of plover nests in the pasture (33 nests).

Finally, during incubation adult Mountain Plovers spent an average of 42.3% (in 1969) and 57.8% (in 1971) of time during the day attending the nest (Graul 1975). This is low compared to other species of Charadriidae that share incubation. Both sexes of Killdeer participate about equally in incubation of their nest (Bailey and Niedrach 1965, Johnsgard 1981). Thus, it seems more likely that a Killdeer would expropriate an unattended (although occupied) Mountain Plover nest than that a Mountain Plover would parasitize a Killdeer nest that was closely attended and defended.

Interspecific nest parasitism among shorebirds is exceedingly rare (Amat 1998; L. W. Oring, pers. comm.). We found no known cases of nest parasitism by Mountain Plovers or Killdeer in the literature. This is the first record in approximately 1130 Mountain Plover nests to contain Killdeer eggs and have a Killdeer incubating [154 Mountain Plover nests found in five years (Graul 1975; Weld Co., Colorado), approximately 400 in ten years (Knopf, pers. comm.; Weld Co., Colorado), approximately 500 in five years (Dinsmore, pers. comm.; Montana), 33 in two years (Sordahl, pers. comm.; Weld Co., Colorado), and 45 in one year (this study; Baca Co., Colorado)].

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SEXUAL SIZE DIMORPHISM OF THE MUSK DUCK

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ABSTRACT.—We examined sexual size dimorphism of a lek-displaying diving duck from Australia, the Musk Duck (*Biziura lobata*). Like other lek-displaying species, Musk Ducks exhibit extreme sexual size dimorphism in addition to structural dimorphism. Body mass ratios (male:female) for Musk Ducks are among the highest reported for birds (more than 3:1). Multivariate analyses of 16 anatomical measurements indicated that body plans of male and female Musk Ducks have diverged isometrically except for the addition of a pendant lobe on lower mandibles of males. Within males, pendant lobe length, depth, and breadth were positively correlated with center rectrix length and bill width. Lobe area also was positively related to bill width, but not to center rectrix length. Lobe breadth and center rectrix length were positively related to overall body mass. Our results suggested that information about male physical quality may be conveyed to other Musk Ducks by parts of the anatomy most conspicuously exposed during sexual advertising displays. In contrast, anatomical features that function in foraging activity showed no sexual differences in anatomical shape relative to other parts of the anatomy that do not serve obvious foraging functions. We argue that foraging niche divergence or use of different food resources, if they have occurred, probably are secondary consequences of sexual size dimorphism. *Received 28 March 2000, accepted 18 August 2000.*

The Musk Duck (*Biziura lobata*) is a lek-displaying diving duck endemic to deep water wetlands, river systems, and coastal oceanic waters of temperate Australia (Frith 1967, Marchant and Higgins 1990, Johnsgard and Carbonell 1996). As an undivided basal lineage distant from other waterfowl, Musk Ducks show marked morphological and ecological convergence with *Nomonyx-Oxyura* stifftail ducks and deep-water divers such as eiders (*Somateria, Polysticta*) and steamer ducks (*Tachyeres*; McCracken et al. 1999; but see Livezey 1986, 1995). Musk Ducks also show extreme sexual size dimorphism.

The heaviest male Musk Duck reportedly weighed 3870 g (Serventy and Whittell 1962), whereas the smallest female weighed 993 g (Frith 1967), more than a three-fold difference in overall body mass. The average size dimorphism ratio (male : female) reported by Frith (1967) for a sample of 535 Musk Ducks was 1.55:1 (max. = 3.14) and ranks sixth among 47 lek-breeding bird species surveyed by Oakes (1992). With the exception of a few other promiscuous anatids (*Asarcornis scutulata,* mean = 1.45, max. = 2.00; *Cairina moschata,* mean = 1.44, max. = 3.64) and two flightless species (*Tachyeres pternes,* mean = 1.43, max. = 1.70; *Anas aucklandica,* mean = 1.43, max. = not available), most waterfowl show average sexual body mass dimorphism ratios well below 1.4:1 (Johnsgard 1978, Madge and Burn 1988, Marchant and Higgins 1990, Dunning 1993).

Observational data (Frith 1967, Marchant and Higgins 1990, McCracken 1999) suggest that male emancipation from parental care and evolution of a lek mating system led to fixation of larger body size and other secondary sexual characters in male Musk Ducks (Fisher 1930, Møller 1990, Zuk et al. 1990). An alternative hypothesis not related to mating system theory is that niche divergence, perhaps driven by intersexual competition for food resources, is responsible for observed patterns of size dimorphism in Musk Ducks (Selander 1972, Nudds and Kaminski 1984, Slatkin 1984). Male and female Musk Ducks differ so greatly in size that the sexes probably occupy different foraging niches; however, little information about diets of this species currently is available (see Gamble 1966). We believe that insight into the forces responsible for Musk Duck sexual size dimorphism can be gained by measuring and comparing size and shape characteristics between sexes (Alisauskas 1987, Webster 1997). If aspects of the mating system primarily are responsible for

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sexual size dimorphism, we predicted that non-isometric patterns of dimorphism would be correlated with secondary sexual features associated with particular advertising displays. For Musk Ducks, the size and shape of the pendant lobe that hangs below the lower mandible or the length of the tail feathers are obvious possibilities because these parts of the anatomy are used almost exclusively in sexual displays (Johnsgard 1966, Frith 1967, Marchant and Higgins 1990, McCracken 1999). If niche divergence has occurred, we predicted that stronger patterns of sexual dimorphism would be evident in the feeding apparatus or other associated anatomical features that would allow one sex to gain access to different food resources than the other.

We tested the null hypothesis that male and female Musk Ducks show no differences in anatomical shape, independent of general body size. We also analyzed patterns of variation among males to evaluate the relative contribution of different body parts towards total size variation and determined whether the size of body parts were correlated with one another. We paid particular attention to anatomical features (e.g., lobe size and shape, tail length, tarsus length, etc.) hypothesized to have evolved for different functions such as sexual display, foraging, and locomotion. Lastly, we examined whether individuals differed in size or shape by capture method. Our measurements are the first for males and females captured at the same locality in more than 30 years and include many features of the anatomy previously not recorded (Frith 1967, Braithwaite and Frith 1969, Briggs 1988).

STUDY AREA AND METHODS

We captured, measured, banded, and released 46 Musk Ducks (29 males, 17 females) at Murray Lagoon, Cape Gantheaume Conservation Park, Kangaroo Island, South Australia (35° 55' S, 137° 25' E) between 11 September 1995 and 19 October 1997. We used three capture methods: night-lighting (31 captures; Bishop and Barratt 1969), baited clover-leaf traps (12 captures; Addy 1956), and walk-in-nest-traps (3 captures; Dietz et al. 1994).

Morphometrics.—We recorded 12 measurements for each captured duck: bill length (±0.1 mm), bill width (±0.1 mm), bill height (±0.1 mm), head length (±1 mm), tarsus length (±0.1 mm), tarsus bone length (±0.1 mm), total length (±5 mm), wing span (±5 mm), wing chord (±1 mm), 9th primary length (±1 mm), center rectrix length (±0.1 mm), and body mass (±50 g). We also measured (±0.1 mm) length, depth, and breadth of lobes on males (females possess only small vestigial lobes; six were measured). Lobes for all but two males (too small to trace) were traced in the field. Lobe outlines subsequently were transferred to dry paper, cut out, and weighed (±0.01 g), whereby the total area (cm^2) of the lobe was calculated by dividing the mass of each lobe outline by the density (g/cm^2) of the paper. We recorded age (hatching year/after hatching year) as indicated by the presence or absence of natal down notches on tail feathers (Bellrose 1980). Wing and tail molts also were recorded.

Statistical analyses.—We used multivariate analysis of covariance (MANCOVA) to test whether morphometric measurements (excluding those describing the sub-mandibular lobe) differed between sexes and capture methods or varied with capture date (PROC GLM; SAS 6.12; SAS Institute, Inc. 1996). Capture methods included in the model were night-lighting and baited clover-leaf traps; three females captured on the nest were omitted from the analysis. We began with a saturated model containing sex and capture method as explanatory variables, capture date as a covariate, and all possible interactions. Nonsignificant interactions and covariates were removed iteratively, starting with the highest order interactions, and the analysis was repeated until a single most parsimonious model containing only sex and capture method was obtained. *F*-values reported from multivariate analysis of variance (MANOVA) were determined using Wilks' λ. Following a significant MANOVA, we used analysis of variance (ANOVA) to test whether individual body measurements differed between sexes and capture methods. We report least squares means and standard errors (±SE) for morphometric variables that differed between capture methods (PROC GLM; SAS 6.12; SAS Institute, Inc. 1996); unadjusted means and standard deviations (±SD) are given in Table 1. In light of significant sexual differences in all measurements ($P < 0.001$), we used the CANONICAL option in the MANOVA statement (PROC GLM; SAS 6.12; SAS Institute, Inc. 1996) to examine the canonical axes that best distinguish the sexes morphologically and determine the relative contribution of each dependent variable to sex separation (see Hatcher and Stepanski 1994). We used a *G*-test to determine if sex ratios differed between capture methods.

To test the null hypothesis that males and females show no differences in anatomical shape, independent of overall body size, we performed principal components analysis (PCA; PROC PRINCOMP; SAS 6.12; SAS Institute, Inc. 1996) using the correlation matrix of the same 12 metric variables to construct one index of overall body size (PC1) and eleven indices of shape (PC2–12). Corresponding principal component scores for each individual were subsequently entered into a MANOVA (PROC GLM; SAS 6.12; SAS Institute, Inc. 1996) to create a single linear model, including sex and capture method as explanatory variables and the 12 principal component scores as response vari-

TABLE 1. Body size measurements (mm or cm^2) and body mass (g) for male and female Musk Ducks at Murray Lagoon, Cape Gantheaume Conservation Park, Kangaroo Island, South Australia, 1995–1997.

Measurement	Male			Female				
	n	Mean ± SD	Range	*n*	Mean ± SD	Range	*P*[a]	CAN1[b]
Bill length	29	40.19 ± 1.00	37.3–42.1	17	35.01 ± 1.23	32.7–37.0	0.001	1.32
Bill width	29	36.30 ± 1.21	34.1–39.1	17	30.15 ± 2.37	28.0–37.6	0.001	0.54
Bill depth	29	34.97 ± 2.26	32.3–43.5	17	28.64 ± 1.09	26.4–30.4	0.001	0.81
Head length	29	103.4 ± 3.0	97–111	17	90.6 ± 3.1	84–95	0.001	0.39
Lobe length	29	71.17 ± 18.18	37.7–102.4	6	33.13 ± 1.80	31.0–36.0	—	—
Lobe depth	29	62.42 ± 21.48	11.6–99.5	6	6.87 ± 1.22	5.0–8.0	—	—
Lobe breadth	29	31.93 ± 4.00	21.7–39.7	6	20.22 ± 0.84	18.7–21.1	—	—
Lobe area	27	37.60 ± 18.32	8.1–69.1	—	—	—	—	—
Tarsus length	29	63.05 ± 2.90	57.7–69.8	17	53.66 ± 2.88	49.1–60.4	0.001	−0.59
Tarsus bone length	29	51.43 ± 2.49	44.5–56.0	17	44.00 ± 2.36	41.0–50.4	0.001	−0.08
Total length	27	664.6 ± 23.6	610–710	15	552.7 ± 17.3	530–580	0.001	0.92
Wing span	26	874.5 ± 41.5	770–960	13	723.8 ± 26.9	650–760	0.001	0.65
Wing chord	26	226.3 ± 8.6	205–240	13	183.7 ± 4.7	175–190	0.001	1.17
9th primary	26	164.6 ± 19.2	130–210	13	126.8 ± 12.2	102–140	0.001	0.36
Center rectrix	27	117.1 ± 9.0	91–130	12	96.2 ± 9.4	75–110	0.001	−0.12
Body mass	29	2560.2 ± 331.3	1700–3100	17	1560.9 ± 245.3	1150–1910	0.001	−0.41

[a] ANOVAs for sex effect were adjusted for capture method (1, 33 df for each test; lobe measurements excluded). Measurements shown in the table were not adjusted for capture method. Molting soft parts not fully grown were omitted from the tests.

[b] Standardized between sex canonical coefficients were adjusted for capture method.

ables (see also Alisauskas 1998). Following a significant MANOVA, we used ANOVA to test whether individual principal components describing size (PC1) and shape (PC2–12) differed between sexes and capture methods.

To analyze anatomical patterns of variation among males, we performed a second principal components analysis and MANOVA (PROC GLM; SAS 6.12; SAS Institute, Inc. 1996) using the same 12 measurements plus the 4 lobe measurements and capture method as the independent variable. We regressed the 4 lobe measurements on each of the other 12 measurements using analysis of covariance (ANCOVA; PROC GLM, SAS 6.12; SAS Institute, Inc. 1996) to determine if lobe dimensions were correlated with size of other anatomical features and whether these relationships differed between Musk Ducks caught by night-lighting or baited clover-leaf traps. Center rectrix length was regressed on all non-lobe measurements using ANCOVA. For both sets of analyses, total length was adjusted for the length of the tail by subtracting the length of the center rectrix.

FIG. 1 Frequency distribution of body mass for adult male (n = 29) and female (n = 17) Musk Ducks captured at Murray Lagoon, Cape Gantheaume Conservation Park, Kangaroo Island, South Australia, 1995-1997.

RESULTS

Variation between sexes and capture methods.—All Musk Ducks measured in our study were after-hatching year birds. Overall body size differed between sexes (MANOVA: F = 37.51, 12, 22 df, $P < 0.001$) and capture methods (MANOVA: F = 3.05, 12, 22 df, P = 0.011). Overall body size did not vary with capture date, and no interaction was significant (all Ps > 0.05). All measurements were significantly larger for males than for females (Table 1, Fig. 1). Measurements contributing the most to sex separation, in order of decreasing contribution included bill length, wing chord, total length, and bill depth (CAN1; Table 1). Wing span and head length showed no overlap in absolute size (Table 1). Measurements contributing the least to sex separation included tarsus bone length and center rectrix length. Three of 12 measurements differed significantly between capture methods (all

TABLE 2. Eigenvectors for principal components analysis of pooled anatomical measurements for male and female Musk Ducks at Murray Lagoon, Cape Gantheaume Conservation Park, Kangaroo Island, South Australia, 1995–1997.

Measurement	Eigenvectors		
	PC1	PC2	PC3
Total length	0.3140	0.1012	0.0279
Wing chord	0.3093	0.0028	0.0823
Bill width	0.3049	0.0475	−0.1889
Bill length	0.3020	−0.1013	−0.1641
Wing span	0.3003	−0.0647	0.2228
Head length	0.2942	−0.1672	−0.2306
Body mass	0.2912	0.0754	−0.3679
Tarsus length	0.2905	−0.2934	0.4080
Tarsus bone length	0.2791	−0.3501	0.4609
Bill depth	0.2704	−0.2666	−0.4971
Ctr. rectrix length	0.2584	0.5314	0.2560
9th primary	0.2407	0.6142	0.0088

other *P*s > 0.05). Musk Ducks caught by night-lighting had longer tarsi than those caught in baited clover-leaf traps (night-lighting least squares mean ± SE = 58.64 ± 0.58 mm, clover-leaf traps = 56.39 ± 0.86 mm; ANOVA: F = 5.26, 1, 33 df, P = 0.028). Ninth primary (night-lighting = 139.6 ± 3.2 mm, clover-leaf traps = 161.5 ± 4.7 mm; ANOVA: F = 16.85, 1, 33 df, $P < 0.001$) and center rectrix (night-lighting = 105.1 ± 1.9 mm, clover-leaf traps = 111.9 ± 2.8 mm; ANOVA: F = 4.44, 1, 33 df, P = 0.043) showed the opposite relationship. Sex ratios also differed by capture method (G = 3.446, 1 df, $P < 0.05$). Of 29 Musk Ducks captured by night-lighting 17 were male and 12 were female (male : female = 1.42:1), whereas 12 males and 2 females were captured in baited clover-leaf traps (male : female = 6.0:1).

Principal components analysis revealed three discernable patterns of variation in pooled male and female Musk Duck anatomical data, excluding lobe measurements. The first principal component (PC1) accounted for 79.2% of observed variation (eigenvalue = 9.51) and related to overall body size, as indicated by positive eigenvectors of approximately equal magnitude for all 12 measurements (Table 2). The second component (PC2) accounted for 6.7% of observed morphometric variation (eigenvalue = 0.80) and corresponded to a decrease in the size of the tarsus relative to the lengths of the 9th primary and center rectrix (Table 2). The third component (PC3) accounted for an additional 3.7% of observed variation (eigenvalue = 0.45) and corresponded to a reduction in the size of the head and overall body mass relative to the size of the tarsus (Table 2). Informative anatomical trends were not evident in PC4–12 (eigenvalues ≤ 0.31). MANOVA indicated that one or more principal components differed significantly between sexes (F = 37.51, 12, 22 df, $P < 0.001$) and capture methods (F = 3.05, 12, 22 df, P = 0.011). Subsequent ANOVAs indicated that differences between sexes were limited to PC1 (F = 422.04, 1, 33 df, $P < 0.001$), and differences between capture methods were limited to PC2 (F = 18.56, 1, 33 df, $P < 0.001$); PC3–12 did not differ significantly between sexes or capture methods (PC3–12, all *P*s > 0.05). Thus, excluding lobe characteristics and a component of morphometric variation related to capture bias (PC2), sexual divergence in Musk Duck morphology was isometric.

Variation among males.—Principal components analysis revealed three patterns of variation among males that may be of biological significance. The first 5 principal components (PC1–5) accounted for 75.2% of the observed morphometric variation and had corresponding eigenvalues of 1.13 or greater. Measurements most highly correlated with PC1 (26.9% of the total variation) were the 4 lobe measurements (Table 3). The next most highly correlated measurements were bill width, body mass, and center rectrix length. Other measurements expected to be associated with flight and diving proficiency (e.g., wingspan, wing chord, 9th primary, tarsus length, tarsus bone) were not highly correlated (PC1 eigenvectors absolute magnitudes ≤ 0.105). Male variation in these measurements instead appeared to be evident in PC2 (19.3% of the total variation), in which tarsus length, tarsus bone length, wingspan, and wing chord measures showed larger correlations than other measurements (Table 3). The third principal component (PC3) made up an additional 11.6% of the total variation in males and differed between capture methods (ANOVA: F = 24.57, 1, 22 df, $P < 0.001$). Lucid anatomical trends were not readily evident in any other principal components, and no other com-

TABLE 3. Eigenvectors for principal components analysis of anatomical measurements for male Musk Ducks at Murray Lagoon, Cape Gantheaume Conservation Park, Kangaroo Island, South Australia, 1995–1997.

Measurement	Eigenvectors				
	PC1	PC2	PC3	PC4	PC5
Lobe area	0.4481	−0.1173	−0.0281	−0.0963	0.0989
Lobe length	0.4431	−0.0544	−0.1412	−0.1526	0.0836
Lobe depth	0.4238	−0.0029	−0.2152	−0.0926	0.0779
Lobe breadth	0.4154	−0.0842	0.0062	0.0276	−0.0285
Bill width	0.2377	0.1885	−0.1369	0.4121	−0.3130
Body mass	0.2282	0.1052	0.4375	0.1580	−0.2197
Ctr. rectrix length	0.1792	0.1720	0.3263	−0.4371	−0.0229
Total length	0.1743	0.2596	0.4465	0.0864	−0.0180
Bill length	0.1689	0.0355	0.0808	0.3086	0.4529
Bill depth	0.1450	0.2606	−0.1546	0.2002	−0.4078
Wing span	−0.1047	0.4444	0.1082	−0.0360	−0.0533
Tarsus bone length	−0.0974	0.4448	−0.1767	−0.1058	0.1572
Wing chord	0.0751	0.3330	−0.1162	−0.3161	0.4166
9th primary	−0.0580	−0.0357	0.5535	0.0030	0.1357
Tarsus length	−0.0257	0.5059	−0.1519	0.0947	0.0321
Head length	−0.0020	−0.0031	0.0255	0.5551	0.4871

ponents differed between capture methods (ANOVAs: all *P*s > 0.05).

The length, depth, and breadth of the lobe were positively related to center rectrix length and bill width (Figs. 2A, 3). Lobe area also was positively related to bill width (Fig. 3) but not to center rectrix length, and lobe breadth was positively related to overall body mass (Fig. 2B). No other linear relationships between lobe dimensions and other body parts were evident (all *P*s > 0.05). Length of the center rectrix, which varied positively with lobe length, depth, and breadth (all *P*s ≤ 0.028; Fig. 2A), was positively related to body mass (Fig. 2B). Length of the center rectrix also varied positively with wing chord in males caught by night-lighting, but not in males caught in baited clover-leaf traps (Fig. 2B). Center rectrix length showed no significant linear relationship to bill width or any other non-lobe measurement (all *P*s > 0.05), and no other measurements showed a capture effect (all *P*s >0.05).

DISCUSSION

Many authors have argued for a causal relationship between sexual size dimorphism and evolution of promiscuous mating behavior (e.g., Darwin 1871, Lack 1968, Payne 1984, Oakes 1992; but see Höglund 1989, Höglund and Sillén-Tullberg 1994). We found that 86% of male and female Musk Ducks showed no overlap in body mass (Table 1, Fig. 1). This level of dimorphism ranks high in comparison with other dimorphic species and is among the highest ever recorded for lek-breeding birds. One possible explanation for the appearance of extreme sexual size dimorphism is that factors related to lek breeding (strong female selection for high quality males or competition among males for limited access to females) led to fixation of larger body size and other secondary sexual characters in male Musk Ducks. An alternative hypothesis, not related to the mating system, is that sexual competition for food resources (foraging niche divergence) led to sexual size dimorphism.

Sexual selection.—Our data indicated that the size of the lobe, width of the bill, body mass, and length of the center rectrix were significant elements of structural variation within male Musk Ducks (Table 3, Fig. 1). Among these, the length, depth, and breadth of the lobe increased linearly with the length of the center rectrix (Fig. 2A). It is not surprising that the lobe and tail feathers showed a significant correlation in this species, because these are the two features of the male anatomy that are prominently displayed during bouts of sexual display activity (Johnsgard 1966, Frith 1967, Marchant and Higgins 1990, McCracken 1999). In the paddle-plonk-whistle-kick display described by Johnsgard (1966) and others, the lobe swells with blood

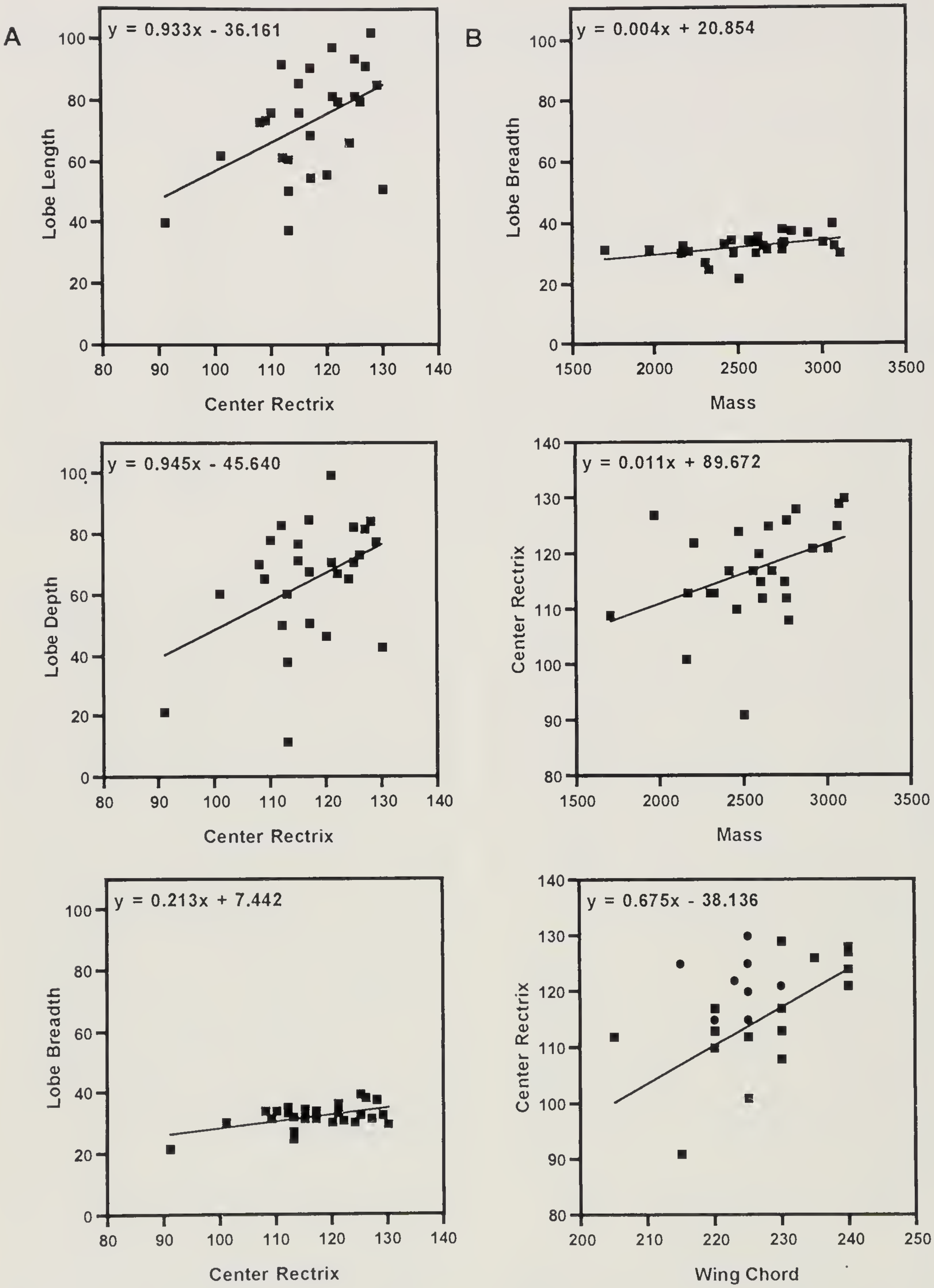

FIG. 2 (A) Relations between center rectrix length and lobe length (F = 7.50, 1, 25 df, P = 0.011, R^2 = 0.23), lobe depth (F = 5.48, 1, 25 df, P 0.027, R^2 = 0.18), and lobe breadth (F = 8.20, 1, 25 df, P = 0.008, R^2 = 0.25) of adult male Musk Ducks captured at Murray Lagoon, Cape Gantheaume Conservation Park, Kangaroo Island, South Australia, 1995-1997. (B) Relations between body mass and lobe breadth (F = 4.62, 1, 27 df, P = 0.041, R^2 = 0.15), body mass and center rectrix length (F = 5.02, 1, 25 df, P = 0.034, R^2= 0.17), and wing chord length and center rectrix length (males captured by night-lighting indicated by squares, F =

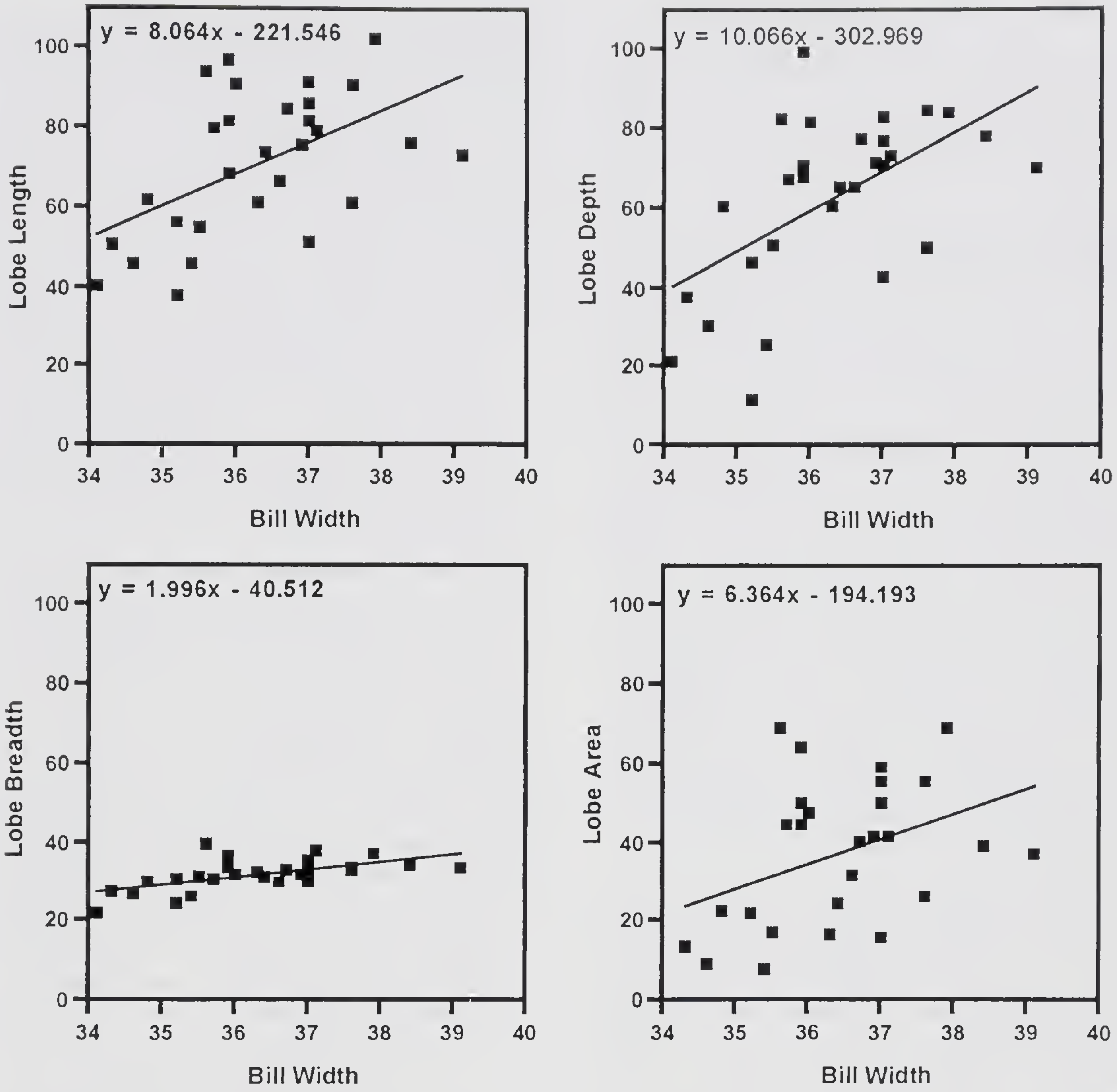

FIG. 3 Relations between bill width and lobe length (F = 10.81, 1, 27 df, P = 0.0028, R^2 = 0.29), lobe depth (F = 12.64, 1, 27 df, P = 0.0014, R^2 = 0.32), lobe breadth (F = 15.34, 1, 27 df, $P < 0.001$, R^2 = 0.36), and lobe area (F = 4.72, 1, 25 df, P = 0.04, R^2 = 0.16) of adult male Musk Ducks captured at Murray Lagoon, Cape Gantheaume Conservation Park, Kangaroo Island, South Australia, 1995-1997.

and is thrust forward rhythmically to accompany coordinated splashing displays and vocalizations. At the same time, the tail is spread wide, repeatedly lifted, dropped to the surface of the water, and cocked over the back. Together, the swollen lobe and spread tail feathers create an unusual spectacle, but what do the lobe and tail feathers signal to other Musk Ducks?

Our data indicated that the size of the lobe is a true indicator of the width across the bill (Fig. 3). Other measurements, including bill length, bill depth, head length, various measures of the wings and tarsi, and adjusted total body length showed no relationships to lobe size. Width of the bill undoubtedly parallels the internal width of the gape and probably is a good estimate of a Musk Duck's ability to

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10.76, 1, 14 df, P = 0.006, R^2= 0.43; males captured by baited clover- leaf traps indicated by circles, F = 0.27, 1, 8 df, P = 0.05, R^2 = 0.03, no regression line) of adult male Musk Ducks captured at Murray Lagoon, Cape Gantheaume Conservation Park, Kangaroo Island, South Australia, 1995-1997.

swallow large food items. The width of the bill also might factor importantly in fights with other males, the ability to seize females for copulation, and the capacity to out-compete other waterfowl for food by inflicting strong bites (see McCracken 1999). A wider gape might reflect the need for a stronger point of attachment of the lower mandible for Musk Ducks with larger lobes, and if larger lobes are more costly than smaller lobes, males that wear larger lobes may exhibit greater fitness (Zahavi 1975, 1977). Although the length of the center rectrix covaried with the dimensions of the lobe, unlike the lobe, it was not positively correlated with bill width. Center rectrix length instead was positively correlated with overall body mass, as was lobe breadth. These observations suggest that additional information about overall body size is presented in the parts of the anatomy most conspicuously exposed during sexual displays. In principle, there are many reasons why females might select males with wider gapes and greater body mass if both traits are advantageous and result in increased fitness to the parents and offspring.

To what extent the size of the lobe, length of the tail, and other anatomical features correlate with age or physical condition is unknown, because no information about growth rates, nutrient allocation, or parasite loads is available for Musk Ducks. If Musk Ducks continue to grow asymptotically beyond their first year of life (and this is very plausible), continued growth and sexual development could contribute to age-related differences in size and social dominance (see Alisauskas 1987). In particular, the size of the lobe and other measurements might be determined by growth during immature stages, with birds that are doing the poorest having proportionately smaller measurements (Møller 1990). Our identification of a capture bias may be evidence of such age-related growth patterns. Perhaps individuals captured by active means (i.e., night-lighting) were younger birds and more prone to capture because of their morphology or physical condition. Sex ratios also showed a capture bias. More than 4 times as many males per female were caught by baited clover-leaf traps than by night-lighting. One explanation for the different sex ratios in the two catches might be that males are socially dominant to females (see also McCracken 1999). Males also may be more active than females and range over greater distances. In either case, documentation of the effects of age and physical condition on morphology and its relationship to social and reproductive status will require that marked Musk Ducks of known age be measured repeatedly over a period of several years. Such a study also could determine whether the size of the lobe can change with time depending on current physical condition or reproductive status.

Other factors that could have influenced sexual size dimorphism include limited and unpredictable access to females and potentially asynchronous female ovulation cycles as a result of an extended breeding season (McCracken et al. 2000). Data supporting this conclusion include classic lek behavior, an excess of male attendants at display bouts, male-biased sex ratios greater than 20:1 in some localities, and patterns of intra-specific aggression (McCracken 1999). Aggression may be reinforced by well-developed mandibular musculature and an unusually sharp nail on the bill. These observations are consistent with the idea that a combination of male and female mediated selective mechanisms have resulted in competitively successful males achieving greater access to receptive females.

Foraging niche divergence.—An alternative explanation of sexual foraging niche divergence as a cause of sexual size dimorphism (Selander 1972, Nudds and Kaminski 1984, Slatkin 1984) is not directly supported by our data. If the niche divergence hypothesis is correct, stronger patterns of sexual dimorphism than we observed should be evident in feeding apparatus and other associated anatomical features (i.e., the shape of the bill and the hindlimbs if underwater swimming efficiency is an important factor in foraging activity). However, we found that male Musk Ducks simply were isometrically larger than females with the addition of a pendant lobe and a longer tail that covaried with the lobe.

The absence of measurable differences in the shape of feeding apparatus, however, can not unequivocally exclude foraging niche divergence as a cause of sexual size dimorphism. Male and female Musk Ducks differ in overall body size by a factor of two to three; thus, size alone should influence rates and modes of nutrient acquisition (Nudds and Kaminski 1984, Nudds and Bowlby 1984). Indeed, male and female Musk Ducks probably occupy different foraging niches. On Kangaroo Island, males occurred more often in nearshore marine environments than did females (McCracken 1999), and with mandibles averaging 14.8–22.1% larger than those of females for any given measurement (bill depth being the greatest), male Musk Ducks probably are capable of capturing and crushing larger, harder shelled prey. At Barrenbox Swamp, New South Wales, twice as many adult males (60%) consumed hard-shelled prey items such as freshwater mollusks as did females (30%; Gamble 1966). Such a relationship, if it is widespread, may confound efforts to distinguish cause from effect in this species.

To understand these patterns more completely, future studies of Musk Ducks will require some paternity work including a heritability analysis of male secondary sexual features, such the size of the lobe, length of the tail, and overall body mass. A study of foraging behavior focusing on prey and habitat selection (e.g., Goudie and Ankney 1988, Hamilton et al. 1999) also would be useful, as would comparisons with ecologically convergent, large-bodied divers such as eiders (*Somateria, Polysticta*) and steamer ducks (*Tachyeres*).

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WINTER FORAGING BEHAVIOR AND PREY SELECTION OF THE SEMIPALMATED PLOVER IN COASTAL VENEZUELA

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ABSTRACT.—We studied wintering Semipalmated Plovers (*Charadrius semipalmatus*) in a mangrove and open bay site in coastal Venezuela to determine whether the minor sexual dimorphism in bill and tarsus lengths in this species was correlated with sexual differences in habitat use, behavior during foraging, and diet. We found no significant differences between the sexes in either habitat use on the mudflats or distances to conspecifics. Neither sex exhibited territorial behavior. Males used significantly more shallow pecks than did females, who used more repetitive probing, particularly at the open bay site. Diets differed between the sexes in the relative abundance of prey in the fecal samples in both habitats, with samples from males containing significantly more dipteran larvae and samples from females containing more copepods and bivalves. Prey size did not vary between the sexes. We documented significant site differences in habitat use, foraging behavior, and diet, probably as a result of differences in prey availability. *Received 10 March 2000, accepted 6 July 2000.*

Few researchers in the tropics have examined the foraging behavior and diet of Neotropical migrant shorebirds, even though overwintering food intake may be an important determinant of survivorship for these birds (Baker and Baker 1973, Schneider 1985, Mercier and McNeil 1994). Foraging behavior and diet in shorebirds can vary as a result of quality of the habitat (Tsipoura and Burger 1999) as well as sexual differences (Durell et al. 1993). Semipalmated Plovers *(Charadrius semipalmatus)* are generalist foragers that feed on small invertebrates, primarily in coastal habitats (Baker and Baker 1973, Skagen and Oman 1996). On the wintering grounds Semipalmated Plovers forage on tidal mud flats that contain a diversity of invertebrate prey (Robert et al. 1989). Semipalmated Plovers exhibit mixed sexual dimorphism: females are 3.7% heavier than males and have proportionately longer wings, but males have bills that are 2% longer than those of females (means of 12.06 mm, 11.85 mm, respectively) and toes that are 2.5% longer than those of females (means of 17.27 mm, 16.84 mm respectively; Teather and Nol 1997).

In other shorebirds the sex with the longer bill can probe more deeply into the substrate for prey than the sex with the shorter bill and can also feed on larger prey (Jonsson and Alerstam 1990). We expected that males, the sex with the longest bill in this species, might forage more frequently on larger prey species and those that occur deeper in the substrate than females. We also expected that males, as a result of their slightly longer toes, might forage more often on softer, wetter substrates, closer to the waterline than females. We tested these predictions by documenting habitat use, foraging behavior, and diet through the use of fecal analyses (Ward 1989, Dekinga and Piersma 1993, Moreira 1994) at two sites (a mangrove and open bay mudflat) in coastal Venezuela (Robert and McNeil 1989).

METHODS

The study was conducted in northeastern Venezuela on the tidal mud flats of the Chacopata Lagoon complex (10° 41′ N, 63° 46′ W), on the northern side of the Araya Peninsula, during October 1997. The lagoon complex consists of many shallow, salt-water bays, rimmed by mangrove swamps and gradually sloping mud-flats. Tidal amplitude in the area is relatively low (averaging only 30 cm), but because of a shallow slope, the mud flats can extend up to 80 m from high to low tide marks (Mercier and McNeil 1994).

The mangrove study site was surrounded by mangrove stands, with approximately 10 m between the high and low tide lines and about 1 km of shoreline. The open bay study site had approximately 4 km of shoreline, was bound by small mangrove stands on two sides, and had 50 m of mudflat exposed at low tide. Because of its greater tidal flushing, the open bay had frequent rafts of decomposing algae wash up on shore at high tide that were not present at the mangrove site.

Semipalmated Plover abundance was at its yearly peak in October (Mercier and McNeil 1994). We sexed birds by the color of their auricular plumage; in females these feathers are the same brown as their backs but in males the feathers are black (Teather and Nol

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1997). Juveniles were distinguished from adults by the presence of buff edges on their wing coverts and solid black bills (Prater et al. 1977). Any adult with ambiguous markings or juvenile was rejected for study (5–10% of the total sample). There was no change in the proportion of birds that we were able to sex or age during the study period.

Feeding substrates were classified with respect to moisture level into one of three categories: dry if above the high tide mark or indistinguishable from areas above the high tide line; damp if there was a noticeable discoloration of the mud or sand as a result of residual water; or wet if a visible film of water remained on the surface. Semipalmated Plovers in our study area were not seen foraging in standing water.

Plovers used two distinct foraging techniques. The first (and most common) was a brief peck into the substrate. The second technique involved a repetitive hammering or probing of the bill into the substrate up to a depth equal to the length of the bill. Both techniques were used by males and females on all substrate types. The two techniques were easily distinguished. Pecking and probing were recorded as single foraging events.

We recorded the behavior of foraging individuals during 5 min observation periods. For each foraging bout the substrate wetness was recorded. We also recorded the distance from the water line for each foraging individual. At the end of 5 min, the species of the closest foraging bird and its distance to the focal individual (estimated as 0–0.9 m, 1–2.9 m, 3–4.9 m, and >5 m) were also recorded.

Data were collected on the first individual located each day at each site. The next bird located of the opposite sex was then observed. When flocks of more than 10 birds were present, we limited our observations to three individuals of each sex per day per site. For flocks less than or equal to 10 birds, only a single bird of each sex was observed to avoid repeatedly selecting the same individuals.

All observations were made using a 25× field spotting scope and 8 × 50 binoculars with the sun at the observer's back. All data were checked for normality using JMP™ ver. 3 for the Macintosh. Count data were analysed using log-linear models and cell χ^2 values were used to test for significant deviations from expected diet values. Linear data were analysed using two-way ANOVA with sex and habitat as main effects. These results are presented as means ± SE. Proportion data were arcsin transformed prior to analysis to normalize data.

Fecal samples were opportunistically collected after witnessing their deposition from individuals of known sex. When viewed through a 25× spotting scope, feces were visible on the mud flats up to 30 m away. Samples from ambiguous sources were rejected. The feces were lifted from the substrate, excluding any surrounding mud or sand, and stored in individual sealed containers containing 70% ethanol for subsequent analysis. The samples were well homogenized when examined (1–2 mo after collection) under a variable magnification (8–50×), stereo, dissecting microscope fitted with an ocular scale. The microscope was also fitted with a 35 mm camera to catalogue any items that were difficult to identify immediately. Prey items were identified to class or family using Gosner (1971) and McAlpine and coworkers (1990).

All items in the fecal samples were counted but length was determined only for unbroken, rigid structures, including the rigid parts of individual prey items. Fecal analysis data were pooled into single samples for each combination of sex and site (Swanson et al. 1974).

RESULTS

Foraging Semipalmated Plovers were observed for almost 200 hours. Intraspecific aggression was observed only once when a foraging adult female displaced a juvenile. Semipalmated Plovers were observed feeding among flocks of small sandpipers (*Calidris mauri, C. pusilla, C. minutilla*), within groups of their own species, or alone during the study. The sexes were not different in their respective distances to conspecifics or other sandpipers, but all Semipalmated Plovers foraged more closely to conspecifics than to sandpipers (distances to conspecific neighbors, males: 1.76 ± 0.25 m, $n = 23$; females: 1.96 ± 0.26; $n = 41$; to small sandpipers, males: 2.86 ± 0.86, $n = 11$; females: 3.17 ± 0.51 m, $n = 18$; species effect: $F_{1,80} = 7.41$, $P < 0.01$; sex effect: $F_{1,80} = 0.36$, $P > 0.05$; no significant interaction). Foraging neighbors were conspecifics in 64 of 93 observations (68.8%).

While the mean distances from the waterline were significantly different between the two sites (site effect: $F_{1,125} = 12.97$, $P < 0.001$), they were not significantly different between the sexes (sex effect: $F_{1,1} = 0.009$, $P > 0.05$: mangrove males: 2.1 ± 0.66 m, $n = 15$; females: 0.7 ± 0.2 m, $n = 15$; open bay males: 4.3 ± 0.8 m, $n = 39$; females: 5.7 ± 0.8 m, $n = 60$; no significant interaction).

Males were observed foraging on dry substrates only twice and females were never seen using dry substrates. Both sexes foraged more on wet than moist substrates [wet substrates: 61/84 observations (72.6%), $G = 13.2$, $P < 0.001$], but there was no significant difference between the sexes in the frequencies with which they used a particular substrate [females: 28/41 (68.2%) observations on wet substrate, males: 25/33 (75.7%) on wet sub-

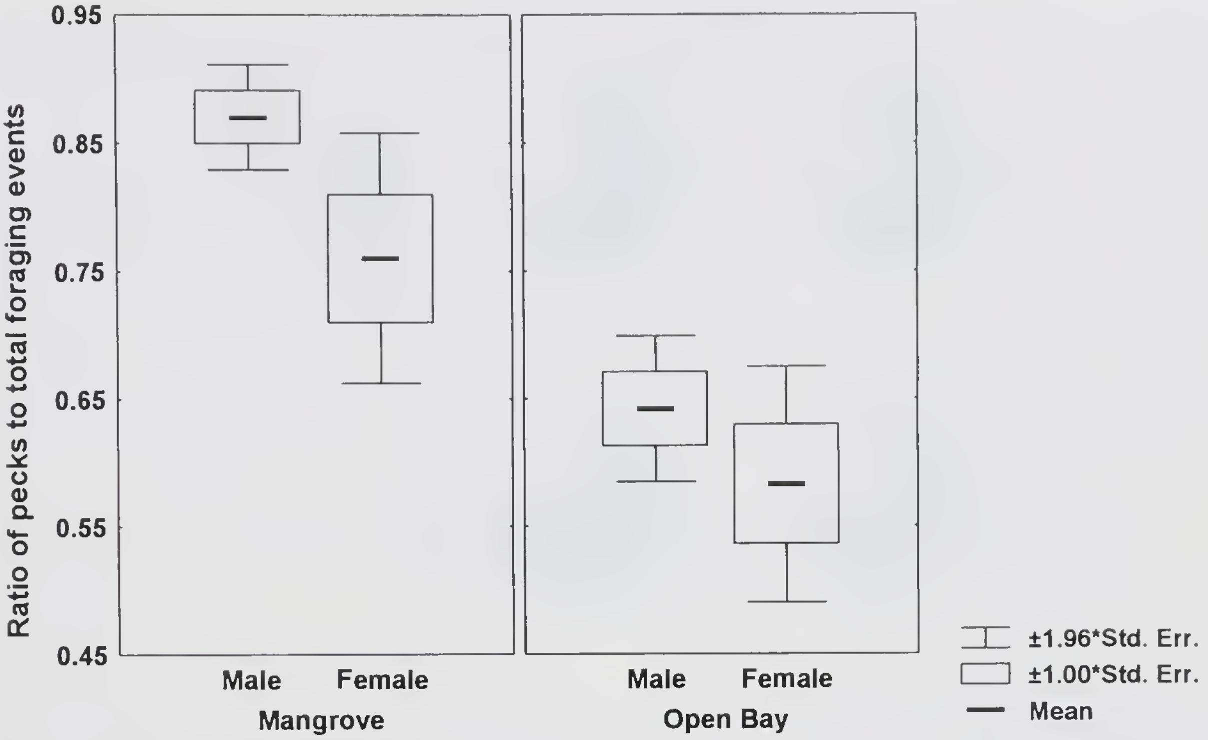

FIG. 1. Ratio of pecks to total foraging events by male and female Semipalmated Plovers on mangrove and open bay mud flats. 1 − ratio = proportion of probing events employed during observation period. Males, mangrove, n = 19 bouts, females, mangrove, n = 15; males, open bay, n = 24, females, open bay, n = 26.

strate; $G = 1.69$, $P > 0.05$], nor was there a site effect ($G = 0.74$, $P > 0.05$).

Foraging rates for males and females were not significantly different, nor did they vary between habitats (mangrove: males 16.8 ± 1.31 events min^{-1}, $n = 19$; females 15.9 ± 2.22 events min^{-1}, $n = 15$; open bay: males 17.5 ± 0.87 events min^{-1}, $n = 24$; females 16.6 ± 0.89 events min^{-1}, $n = 26$; sex effect: $F_{1,80} = 0.76$, $P > 0.05$; site effect: $F_{1,80} = 0.504$, $P > 0.05$; no significant interaction). The ratio of pecks to the total number of feeding events during the observation period was significantly larger for males than females at both sites, with males using fewer probes than females and both sexes using significantly more pecks (and fewer probes) as a proportion of total foraging events at the mangrove site than at the open bay (sex effect: $F_{1,80} = 4.54$, $P < 0.04$; site effect: $F_{1,80} = 30.8$, $P < 0.001$; no significant interaction; Fig. 1).

Individual and whole prey items were recognizable in the fecal samples, often in great numbers. Adult insects were present in almost all fecal samples (38/39, 97.4%) but were usually too fragmented to count individuals. Bivalve mollusks were the next most common prey item (179 individual prey, 22/30 samples, 56.4%) followed by larvae of flies from the family Dolichopodidae (long-legged flies; 380 items, 20/39 samples, 51.3%), copepod crustaceans (323 prey, 22/39 samples, 56.4%), adult Corixidae (too fragmented to count individuals, 15/39, 38.5%), and Canacidae fly larvae (74 individual prey, 9/39 samples, 23.1%). Gastropods (137 individuals, 2 samples), amphipods (1 individual, 1 sample), isopods (1 individual, 1 sample), fiddler crabs (*Uca thayeri*; too fragmented to count, 3 samples) and an unidentified shrimp (Decapoda, 1 sample) were of minor importance in the diet.

The number of prey items that occurred in fecal samples did not differ between the sexes [sex effect: $F_{1,35} = 3.49$, $P < 0.07$; analysis performed on log-transformed data; mangrove: males' mean = 15.1 prey items (95% CI: 10.9–21.0), $n = 13$ samples; females' mean = 28.1 (95% CI: 19.4–40.7), $n = 14$, open bay: males' mean = 9.1 (95% CI: 5.6–14.4), $n = 6$; females' mean = 10.1 (95% CI: 6.6–15.5), $n = 6$] but there were significantly more prey items in fecal samples from the mangrove than from the open bay site (site effect: $F_{1,35} = 15.5$, $P < 0.001$; no significant interaction).

None of the prey items that were frequently found and measured in the fecal samples showed any significant differences in size be-

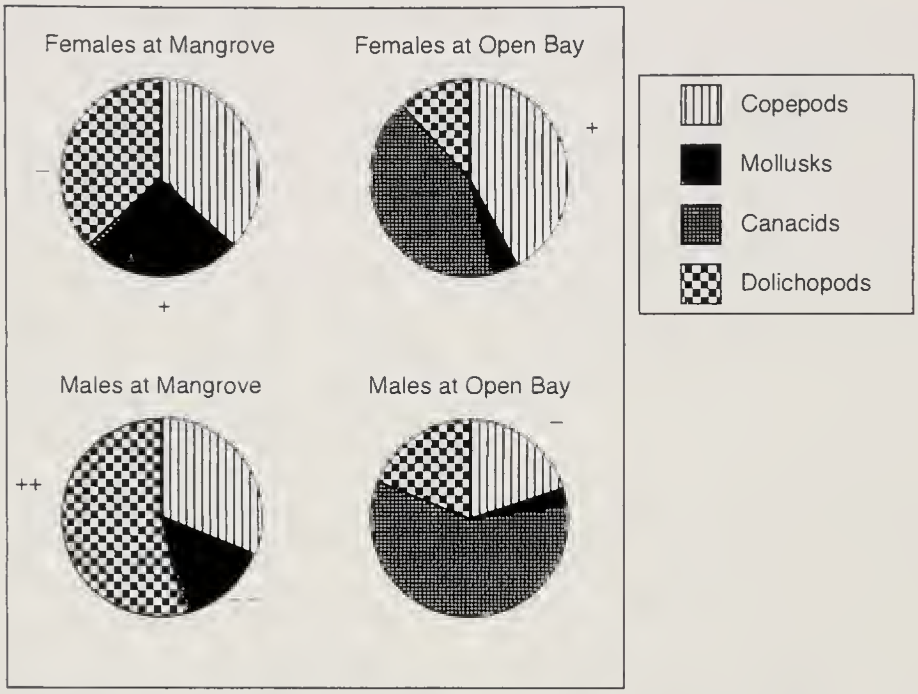

FIG. 2. Proportions of total prey items of four different prey found in fecal samples from males and females at mangrove and open bay habitats. Samples consist of pooled samples from 13 male (232 prey items) and 14 female (481 prey items) fecal samples from the mangrove site, 6 male (59 prey items) and 6 female (65 prey items) fecal samples from the open bay. + and − indicate largest deviations from expected when comparing the two sexes within a habitat (see text for values).

tween the two sexes [Dolichopodidae larvae (length of cephalopharyngeal skeleton): males, 0.58 ± 0.02 mm, $n = 108$; females, 0.58 ± 0.02 mm, $n = 157$; Canacidae larvae (distance between dorsal and ventral cornu of cephalopharyngeal skeleton): males, 0.053 ± 0.001 mm, $n = 60$; females, 0.052 ± 0.001 mm, $n = 16$; bivalve molluscs (longest axis of shell): males, 0.52 ± 0.02 mm, $n = 45$; females, 0.53 ± 0.02 mm, $n = 126$; copepod crustaceans (body length): males, 0.42 ± 0.01 mm, $n = 111$; females, 0.42 ± 0.02 mm, $n = 21$: t-tests, all comparisons between sexes, $P > 0.05$].

For both sexes, the beach flies (Canacidae larvae) were virtually absent from fecal samples collected from the mangrove habitat, whereas this group of insects formed a numerically important part of the fecal samples at the open bay site (Fig. 2). The long-legged flies (Dolichopodidae) formed a numerically large proportion of the diet for both sexes at the mangrove site. The relative proportions of prey items of different categories found in all fecal samples (combined because little individual variation within sex and habitat group) varied significantly between the sexes both at the mangrove site ($G = 15.9$, $P < 0.001$) and at the open bay ($G = 13.8$, $P < 0.001$; data from each habitat analyzed separately because of significant interaction between site and sex). The largest contributions to the deviations from expected in this analysis suggested that fecal samples of males foraging at the mangrove site contained more dolichopods (cell $\chi_1{}^2 = 6.16$, $P < 0.05$) and fewer mollusks than expected (cell $\chi_1{}^2 = 7.07$, $P < 0.05$) whereas fecal samples of females at this site contained no significant differences in mollusks (cell $\chi_1{}^2 = 2.97$, $P > 0.05$) or in dolichopods (cell $\chi_1{}^2 = 3.41$, $P > 0.05$; Fig. 2). At the open bay the greatest deviations to the model were from females foraging more on copepods (cell $\chi_1{}^2 = 2.10$, $P > 0.05$) and males less (cell $\chi_1{}^2 = 2.32$, $P > 0.05$) although only the full model was significant. When contrasting the consumption of all fly larvae with hard-shelled prey like copepods and crustaceans, females consumed higher proportions of these prey than males in both habitats [females at mangrove site: 128/311 (41.1%) total prey items consisted of copepods and bivalves, males at mangrove site: 104/402 (25.8%); $G_1 = 18.6$, $P < 0.001$; females at open bay: 45/80 (56.3%) of prey consisted of copepods and bivalves, males at open bay: 14/44 (31.8%); $G_I = 6.92$, $P < 0.01$].

DISCUSSION

We found minor differences in the foraging behavior and diet of male and female Semipalmated Plovers that do not seem to be explained by the very small differences in bill length between the sexes. We predicted that males, with their longer bills, might forage on larger prey items than females. We did not find support for this prediction; the mean sizes of the rigid structures of the prey found in the fecal samples were sometimes identical.

The behavioral differences in foraging that we documented appeared opposite in direction to our prediction; females were more likely to use probing than were males, the method that appeared to result in deeper penetration into the substrate by the bill. Males fed more often on dipteran larvae (more than 66% of all diet items in both habitats), a prey that was primarily buried in the substrate (McNeil et al. 1995), whereas females fed equally on this insect group and bivalve mollusks and copepods, the latter two items occurred primarily on the surface (McNeil et al. 1995). A study on foraging oystercatchers in Australia suggested that repetitive hammering (or probing) was used to capture hard-shelled prey such as crustaceans, bivalves, and gastropods (Lauro and Nol 1995). In our study the prey items were too small to associate with a particular foraging method and this link could only have been accomplished if we had been able to obtain a longer record of the foraging behavior of the birds prior to defecation. The repetitive hammering into the substrate that we observed in as many as 35% of all foraging events may have caused the slight bill reduction in females as a result of greater wear (Hulscher 1985).

Our findings on substrate preference support previous observations on migrating Semipalmated Plovers by Recher (1966) and Burger and coworkers (1977), who found that plovers tended to spend equal amounts of time on damp and wet mud, while largely avoiding dry areas and areas submerged by water. We found no difference in the substrate preference of male and female Semipalmated Plovers, nor did we find a difference in the distance that males and females foraged from the waterline. Therefore, we also rejected the hypothesis that the minor differences in toe length between the sexes were related to differential preference for substrate wetness. The strong site effect we observed in distance to the waterline reflected the steeper slope of the mangrove site with its smaller moist and wet zone. The reason for the sexual dimorphism in this character remains unknown but may be related to differences between the sexes in migratory behavior, of which little is known. Sexes have never been identified in migratory flocks.

Semipalmated Plovers tend to form loose, conspecific foraging aggregations and were generally not observed foraging alone. This behavior and the absence of any overt intraspecific aggression suggest that there is little aggressive behavior on the wintering grounds in early fall. This agrees with other observations from northern Venezuela (Morrier and McNeil 1991), but contrasts with observations from coastal Peru at the end of the overwintering period, in late March, when intraspecific competition might be expected as food resources are depleted (Myers and McCaffery 1984). The diet partitioning that we documented is presumed to have arisen during a period when food resources were limited (Shine 1989).

The open bay mudflats apparently contained more of the fly family Canacidae as indicated by their much greater abundance in fecal samples from both males and females from this habitat. This family is almost exclusively restricted to tidal habitats (McAlpine et al. 1990). By contrast, bivalve mollusks were more common in the feces of birds foraging in the mangrove site. Given the differences that we observed in numbers of items in fecal samples of birds foraging at the two habitats, there may also be important energetic consequences of this variation in habitat quality (Goss-Custard et al. 1991, Tsipoura and Burger 1999).

Previous researchers of the prey community in coastal Venezuela employed sampling methods that selected only items longer than 1.0 mm (Robert and McNeil 1989, Mercier and McNeil 1994, McNeil et al. 1995). Many of the whole food items in the fecal samples we collected were less than 1 mm, indicating that estimates of available prey for Semipalmated Plovers (and probably some of the smaller sandpipers) must include these size ranges. Baker (1977) found an average prey size of 5 mm in stomach samples of Semipalmated Plovers collected on the Arctic breeding grounds. The abundance of bivalves and copepods in the samples we analyzed in the range of 0.5 mm suggests a mean prey size of smaller than 5 mm at our site, although this conclusion awaits further work on reassessing prey abundance at this overwintering site.

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FRUGIVORY OF SALVIN'S CURASSOW IN A RAINFOREST OF THE COLOMBIAN AMAZON

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ABSTRACT.—We report the diet and the fate of seeds ingested by a family group of Salvin's Curassow (*Mitu salvini*) in Colombian Amazon. The study group consumed 123 plant species from 41 families. Of these, 106 species provided fruits, 21 seeds, 7 cotyledons, 19 flowers, and 9 leaves. Many species of invertebrates and vertebrates were also consumed. During the 14 months about 70% of the diet of each individual was composed of fruits. However, there was considerable temporal variation in diet composition and fruits were not always the most exploited item. Salvin's Curassow acts mainly as a seed predator (67% of the species eaten) on seeds longer than 5 mm but as a seed disperser (28% of the species eaten) for seeds shorter than 5 mm long, which were only rarely and opportunistically exploited. The remaining fruits eaten (5% of the species consumed) were neither dispersed nor predated. As a result of our study, we propose that Salvin's Curassows are mainly seed predators because most seeds ingested by the study group were preyed upon, and seed size was critical in determining seed fate. *Received 14 March 2000, accepted 22 August 2000.*

Curassows, chachalacas and guans (family Cracidae) are large Neotropical forest-dwelling birds that reach their greatest diversity in the Amazon region (del Hoyo et al. 1994, Strahl et al. 1997). They are an important component of the avian biomass in Neotropical bird communities (Terborgh 1986a, Strahl et al. 1997) and provide substantial amounts of protein for rural and Indian people (Silva and Strahl 1991, Vickers 1991, Thiollay 1994). Being extremely sensitive to overhunting and deforestation, cracids are one of the most threatened bird groups in Latin America (Collar et al. 1992, Galetti et al. 1997, Strahl et al. 1997) and can therefore be used as indicators of these two forms of human activity (Silva and Strahl 1991, Strahl and Grajal 1991).

The role of Curassows in seed dispersal and predation is unclear (Levey 1994). Some authors considered them fruit pulp consumers and assumed them to be high quality seed dispersers (Silva and Strahl 1991, Strahl and Grajal 1991), whereas other authors reported them to be important seed predators (Moermond and Denslow 1985, Érard and Sabatier 1986, Terborgh 1986a, Peres and van Roosmalen 1996).

The Salvin's Curassow (*Mitu salvini*) is a large (ca 2.5 kg), terrestrial cracid that occurs in southwestern Colombia, eastern Ecuador, and northeastern Peru (Delacour and Amadon 1973, del Hoyo et al. 1994, Strahl et al. 1997). Little is known about its natural ecology (Santamaría and Franco 1994, Jiménez et al. 1998, Yumoto 1999) or its population densities (Hedemark Jonhson 1993, Santamaría and Franco 1994).

Here we report the feeding ecology and the fate of seeds ingested by a family group of Salvin's Curassows. This constitutes the first long-term study on curassows based on direct field observations.

METHODS

Study site.—The study was carried out on the eastern border of Tinigua National Park, in the northern Colombian Amazon. The base camp was located in lowland tropical rainforest on the west bank of the Duda River (2° 40′ N, 74° 10′ W, elevation 350 m). A riparian forest occurs along the banks of the river but is replaced towards the interior by a forest that is inundated during the rainy season. The terrain in the higher zones is undulating, drained by small channels and is basically a terra firme habitat with a 20–25 m canopy. Annual rainfall is approximately 2600 mm and highly seasonal, with a dry season from December to March. The average minimum and maximum temperature are 21.1° C and 28.7° C (Hirabuki 1990, Kimura et al. 1994, Nishimura et al. 1995). Phenology data obtained between March 1990 and February 1991 indicate that fruit production varies seasonally in the study area, peaking in April, followed by a gradual

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decline, reaching its lowest abundance at the end of the rainy season in November (Stevenson et al. 1998).

Study group.—Observations were focused on one pair of *Mitu salvini* that had been habituated to observers between August 1990–July 1991. Despite the physical similarity between males and females, individuals were identified by subtle morphological characters (smaller body and bill in the female) and sex-specific vocalizations. The pair moved through the forest together, usually with the male in the lead. The home range was approximately 150 ha and food was obtained primarily from the forest floor (Santamaría and Franco 1994). A chick hatched in April 1993 and remained with the pair for ten months (February 1994) until the adults aggressively expelled it.

The field study was conducted between September 1992 and February 1994 and included a single reproductive cycle of the pair: the pre-reproductive period (October–November 1992), the reproductive period (January–April 1993), and the chick rearing stage (May 1993–February 1994). No observations were made in December 1992 and July–August 1993.

The family group was observed from 5:40/6:00 to 17:30/18:20, from 3–5 meters away. Throughout the day, data were recorded using a focal sampling method (Martin and Bateson 1993). Observations were alternated daily among male, female, and young, resulting in three to seven days of observation per individual per month. In total, 2522 hours of observation were accumulated over 185 days.

Diet composition.—Foods ingested by the group were classified into fruits, seeds, cotyledons, flowers, leaves, animals (vertebrate and invertebrate), unknown material, and other. The category other included roots, water, stones, and earth [soil and earth from ant nests (*Atta* sp.)].

Monthly diet composition was estimated by recording the time invested in foraging on each food category (expressed in percentages). This was based on a continuous sampling (Martin and Bateson 1993) of the foraging activity of focal individuals. This activity included searching for and consuming food items. Curassows repeatedly visited a foraging patch and remained there for different amounts of time (Santamaría and Franco, unpubl. data). A foraging patch is defined as the projected area of the tree producing food.

Diet diversity.—Each tree used by the group was marked with a numbered label. Botanical collections were made for species identification by specialists. Invertebrate samples were preserved in 70% ethanol for later identification. The data on diet diversity were complemented by observations of the authors conducted on the same pair between August 1990–June 1991.

Seed dispersal and predation.—Fecal samples (n = 1245) from the focal individual were gathered daily (n = 185 days). Seeds were retrieved by straining the feces through 0.5 mm brass sieves and identified against a reference collection. Because *Mitu salvini* does not regurgitate seeds, all seeds contained in the fecal samples were considered to be dispersed, whereas seeds from consumed fruits that did not appear in the feces were classified as preyed upon. Here, the quality of the dispersion by these birds is not considered because the viability of dispersed seeds was not studied. Because seed length seemed to affect the fate of seeds ingested, we measured seed lengths from Curassows' feces, the foraging patches, and used lengths in the literature (Stevenson et al. 1999).

RESULTS

Composition and temporal variation in diet.—About 70% of each individual's diet was composed of fruits, 10% of seeds, and each of the other categories each less than 5%. This pattern varied month to month and among individuals. For both the male and female, the time foraging for fruits varied from 60–96% during ten months of the study (Fig. 1A, B). Diet composition differed dramatically during two separate two-month intervals. In April–May 1993, the time spent foraging for seeds and cotyledons increased while the time foraging for fruits decreased. In January–February 1994, fruits and seeds were ingested in similar proportions of time, while the amount of time foraging for animals increased considerably (Fig. 1A, B).

The time spent foraging for leaves was low (0.5–6%) but constant, while the time invested in ingesting flowers varied seasonally (Fig. 1A, B). In October–November 1993 and 1994, the time foraging on flowers increased because the group intensively foraged on inflorescences of *Carludovica palmata* (Cyclanthaceae).

During the first months of the chick's development (April–May), its diet was composed primarily of animals (24–38%), cotyledons (15–28%), fruits (16–26%), and seeds (9–12%; Fig. 1C). Thereafter, its diet was similar to those of the adults. During five months the birds spent much time foraging for fruits (70–91%), while in two months (January–February 1994) they showed an increase in time spent foraging for animals (6–18%) and fruits and seeds (36–42% and 36–38%, respectively; Fig. 1C).

Diet diversity.—A total of 123 plant species, representing 41 families, was exploited by the group. Of these, 106 species were recorded for fruits (ripe and unripe), 21 for seeds (ripe and unripe), 7 for cotyledons, 19 for flowers, and 9 for leaves (Table 1). The family containing the largest number of spe-

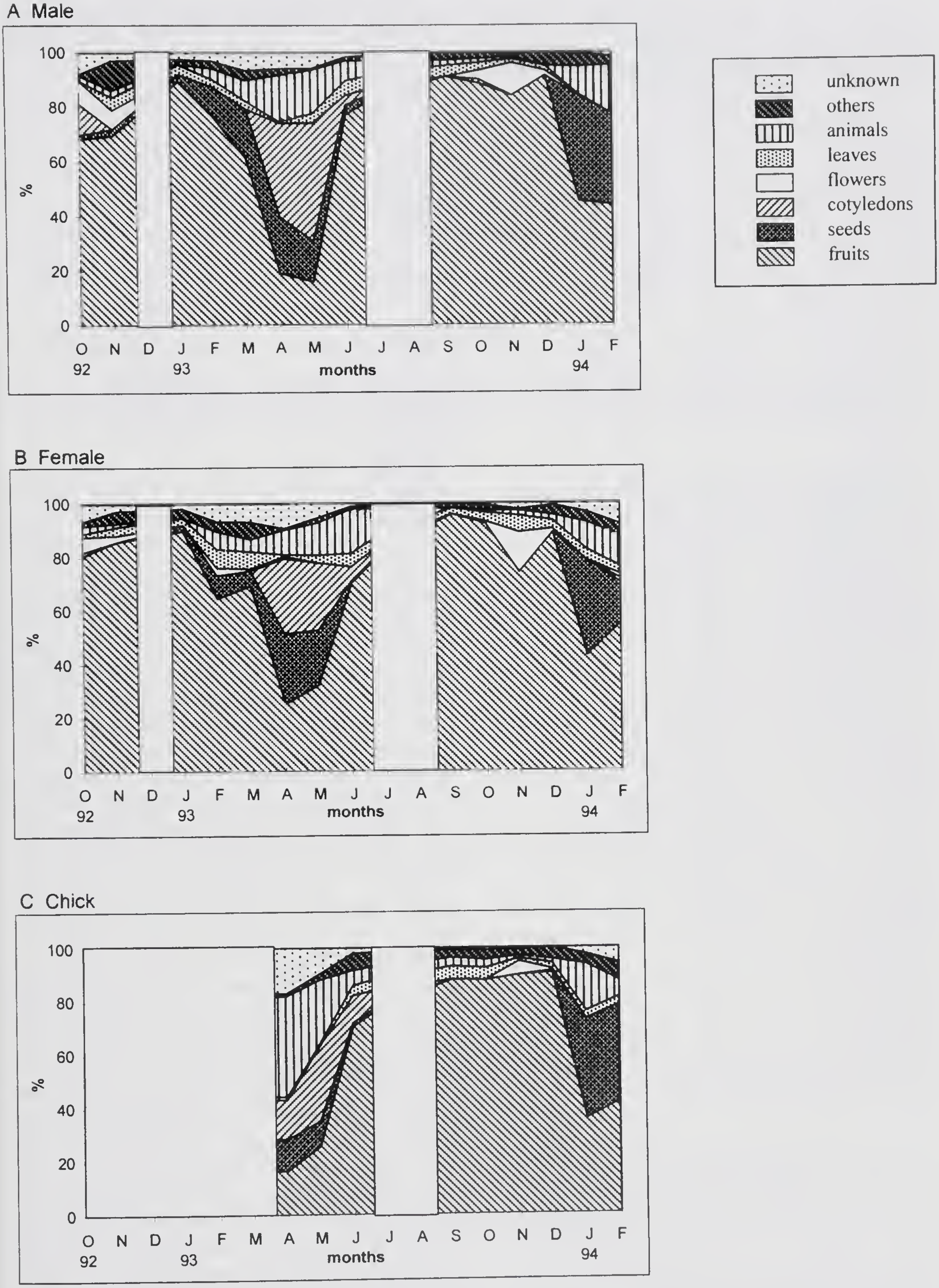

FIG. 1. Monthly variation in the percentage of time foraging on different food categories per individual October 1992–February 1994.

TABLE 1. Number of species per family exploited and food types consumed by the study group August 1990–June 1991 and October 1992–February 1994.

Family	No. of species	Food category[a]
Acanthaceae	2	Fl, L
Annonaceae	2	F
Apocynaceae	4	F, S, C, Fl
Araceae	6	F, Fl
Arccaceae	6	F, Fl
Araliaceae	1	F
Bignoniaceae	2	F, S
Burseraceae	4	F, S, C
Capparaceae	3	F, Fl, C
Caricaceae	1	F, Fl
Cecropiaceae	5	F, S, C
Commelinaceae	1	F
Clusiaceae	3	F, S, Fl
Costaceae	2	F
Cyclanthaceae	1	F, Fl
Euphorbiaceae	1	F
Haemodoraceae	1	F, Fl
Heliconiaceae	4	F
Hippocrateaceae	1	F
Lauraceae	4	F
Lecythidaceae	2	F, S
Marantaceae	3	F, Fl
Melastomataccae	7	F, L
Meliaceae	4	F
Menispermaceae	1	F
Mimosaceae	6	F, S, C
Moraceae	13	F, S, C, Fl
Myristicaceae	1	F
Myrtaceae	1	F, S
Poaceae	1	S
Polygonaceae	1	F
Rubiaceae	12	F, Fl, L
Sapindaceae	3	F
Sapotaceae	3	F, S
Sterculiaceae	3	F
Strelitziaceae	1	F
Solanaceae	1	F
Theophrastaceae	1	F
Tiliaceae	1	F
Verbenaceac	1	L
Violaceae	3	F, S, Fl

[a] Fl = flower, L = leaf, F = fruit, S = seed, C = cotyledon.

cies exploited for fruits (13), seeds (5), and cotyledons (2) was Moraceae. Rubiaceae fruits were represented with 11 species. The greatest number of species used for flowers and leaves were in the Arecaceae (4) and Rubiaceae (3) families, respectively.

It was possible to collect all plant species used for fruits, seeds, and flowers but not for those used as leaf and cotyledon resources. Animals ingested could not always be identified because they were difficult to collect. Nevertheless, many animal species were eaten by the group (Table 2). Both invertebrates and vertebrates were hunted by the curassows and some vertebrate carcasses were scavenged. The carapace of an armadillo was repeatedly visited by the curassow pair before beginning incubation. The nests of several bird species were raided and eggs as well as chicks were eaten. Occasionally, the group joined bird flocks of army ant followers for up to two hours, capturing invertebrates flushed by the ants.

TABLE 2. Invertebrates and vertebrates ingested by the study group between August 1990–June 1991 and October 1992–February 1994.

Invertebrates	Vertebrates
Terrestrial snails	Frogs (adult alive)
Worms	Snakes (adult alive)
Amblipigy, spiders	Pigeons (eggs)
Terrestrial crabs	Ground-Doves (eggs)
Centipede	Tinamous (chicks and eggs)
Millipede	Hummingbirds (chicks and eggs)
Beetles	Trushes (chicks)
Ants (several spp.)	Armadillos (carapace and bones)
Termites	Agouti (bones)
Moths and caterpillars	Rats (alive)
Dragonflies	Bats (dead)
Grasshoppers, buzzers, mantids	
Cockroaches	

Feeding behavior.—Between January–June, the group followed a moving foraging pattern (sensu Zhang and Wang 1995). This behavior was characterized by patrolling various fruiting trees and remaining at each one for short periods (5–20 min). By contrast, August–December few canopy trees had large fruit crops and the group followed a stationary-feeding pattern (sensu Zhang and Wang 1995). This behavior was characterized by the consumption of fruits from a single canopy tree, with the birds remaining for 1–20 consecutive days foraging and resting under or near the tree. They also defended the foraging patch from a Black Curassow group (*Crax alector*). The stationary feeding pattern was associated with *Clarisia racemosa* (Moraceae)

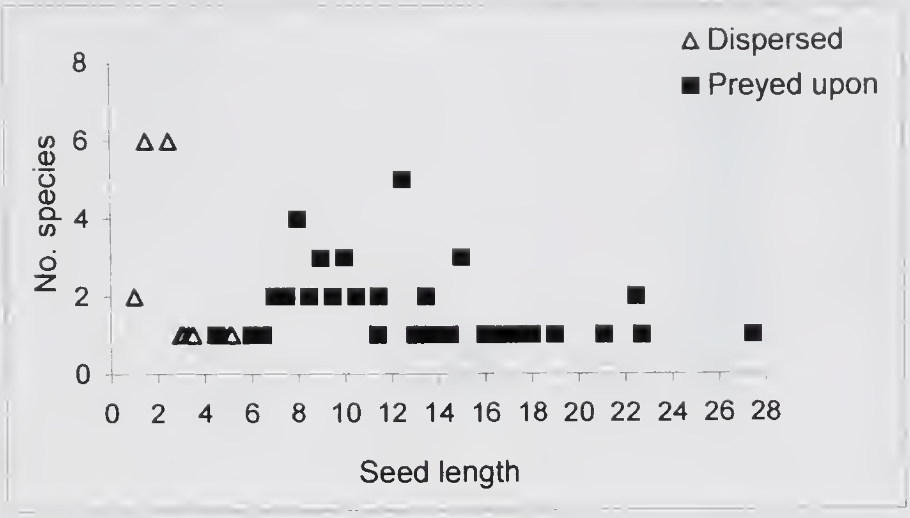

FIG. 2. Number of species dispersed and preyed upon, according to seed length. Seed lengths based on seeds taken from curassow's feces and the foraging patches and from Stevenson and coworkers (1999).

and *Cupania cinerea* (Sapindaceae; August–September 1990), *Talisia intermedia* (Sapindaceae; November 1992) and *Guarea guidonia* (Meliaceae; September–November 1993).

In October 1992, none of the canopy trees used by the curassows produced fruit within the group's home range. Their response to this scarcity was to patrol the forest daily using long transects and investing much time in foraging (an average of 8 hours) but little time in resting. *Heliconia* spp. (Heliconiaceae) fruits and *Carludovica palmata* (Cyclanthaceae) inflorescences were the principal food sources during this time.

To obtain cotyledons, curassows concentrated their foraging under a tree they had previously exploited for fruits and seeds. Typically they pulled up seedlings with their beaks and cut and ate the cotyledons, but occasionally cotyledons were consumed without pulling up the seedlings.

The cracids ate not only young leaves but also mature leaves from understory plants and forest floor. The group always ingested young and mature leaves of *Trichanthera gigantea* (Acanthaceae) after consuming fruits of *Guarea guidonea* (Meliaceae).

Fate of ingested seeds.—The whole fruit (pulp and seed) was ingested in most cases, except for six species. Of 109 fruits and seeds consumed by the curassows, 30 species (28%) of seeds were dispersed by endozoochory, 73 species (67%) of seeds were destroyed, and only the pulp was consumed in 6 species (5%).

Damaged and undamaged seeds of *Geophila macropoda, Psychotria psychotriaefolia,* and *Psychotria muscosa* (Rubiaceae) were retrieved from the feces. Large quantities of stones, red aril fragments of *G. guidonea,* armadillo shell, and insect exoskeletons were also recovered from feces. Seeds of *Gustavia* sp. (Lecythidaceae), *Inga* sp. (Mimosaceae), *Castilla ulei,* and *Pseudolmedia* sp. (Moraceae) were eaten from the ground and the feces of two primates (woolly monkey, *Lagothrix lagotricha;* spider monkey, *Ateles belzebuth*). This suggests that Salvin's Curassow is a post-dispersal seed predator.

Species that were preyed upon were characterized by having fruits with one or two large, oily seeds embedded in little pulp or surrounded by an aril. The seed lengths were 6–30 mm [$\bar{x}$ = 12.69, ± 4.78 (SD), n = 52; Fig. 2), except for *Rinorea lindiana* seeds ($\bar{x}$ = 4.5). Seventy-eight percent of species preyed upon were from canopy and subcanopy trees, 16% from understory plants, and 6% from lianas and epiphytes (Fig. 3). Several species represented a primary resource in the group's diet. During July–December (stationary feeding pattern), the group's diet consisted primarily of species whose seeds were digested (*Clarisia racemosa, Cupania cinerea, Talisia intermedia, Guarea guidonia*). In contrast, dispersed species were occasionally and opportunistically consumed. The seed lengths were 2–5 mm ($\bar{x}$ = 2.68 ± 1.27, n = 23; Fig. 2). Approximately 70% of the species were small understory plants (Fig. 3), with small,

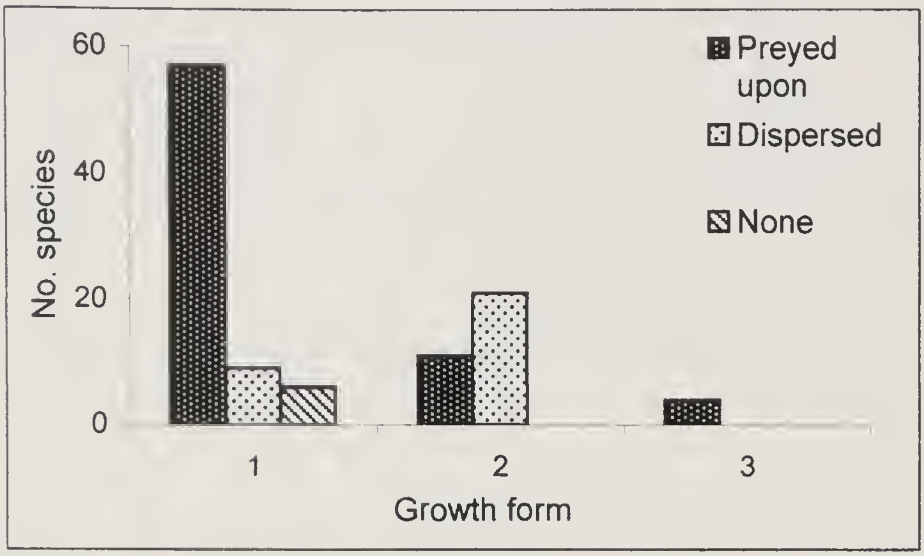

FIG. 3. Number of species dispersed, preyed upon, and not eaten (none) based on the growth form of each species. 1 = canopy and subcanopy trees, 2 = understory plants, 3 = lianas and epiphytes.

juicy fruits containing small seeds (2–5 seeds per fruit) and principally Rubiaceae. The other 30% were from trees 10–25 m tall (one hemiepiphyte species; Fig. 3), that had large fruits with many small seeds embedded in abundant pulp.

DISCUSSION

Previous researchers have classified curassows as chiefly vegetarians (Delacour and Amadon 1973, Torres 1989, del Hoyo et al. 1994), whereas others have considered them to be strictly frugivorous (Silva and Strahl 1991, Strahl and Grajal 1991); some authors reported them to be granivorous (Terborgh 1986a, Terborgh et al. 1990) or seed-eating frugivores (sensu Moermond and Denslow 1985). We found that Salvin's Curassow is mainly a seed predator, digesting the seeds of 67% of the plant species it consumed. This suggests that it is the seeds and not the pulp that is the desired food. The group had a broad diet and spent considerable time foraging for resources other than fruits. Nevertheless, group movements inside the forest seemed to be determined by the location of fruiting trees. Therefore, we suggest that this species should be considered a seed-eating frugivore (sensu Moermond and Denslow 1985) that requires other types of food (fauna, leaves, and flowers) to complement its diet and to satisfy its metabolic requirements.

The availability of high quality resources (seeds and cotyledons) coincided with the reproductive period and hatching of a chick in April. This was also the time the birds took the greatest amount of animal matter. Typically birds feed their chicks predominantly with animal protein during the first months of life to guarantee their rapid growth and development (Morton 1973). Birds require calcium for eggshell production, which can be obtained from grit and mammal bones (MacLean 1974). This could explain why, before incubation (February–March), the study group spent considerable time foraging on an armadillo carcass and bones.

Our results indicate that Salvin's Curassows have a high digestive capability. This ability is due to the powerful, muscular gizzard with a rough interior surface, which allows these birds to crush hard seeds. Small stones and coarse sand appear to serve as grit for grinding because they were always found in the feces analyzed during all of the months sampled.

Our data suggest that the fate of seeds ingested may be determined by their size. Small seeds (<5 mm) were found to pass unharmed through the digestive tract, while larger seeds (>5 mm) were destroyed. We cannot say that small seeds are not digested, but small seeds were more commonly found in the species' feces. Yumoto (1999) reported that Salvin's Curassow dispersed only 6–10% of the small seeds (<5.5 mm) it consumed from two plant species (*Geophila repens,* Rubiaceae; *Ficus sphenophylla,* Moraceae). Seed predation has also been observed in the Black Curassow (*Crax alector*; Érard and Sabatier 1986) and

Amazonian Razor-billed Curassow (*Mitu tuberosa*; Peres and van Roosmalen 1996).

Regular folivory, which is rare in birds (Morton 1978), suggests that the study group required some of the nutrients present in vegetation. Leaves are a source of proteins, but they are difficult to digest because they are high in structural carbohydrates and they contain a variety of toxic compounds (Lambert 1998, Milton 1998). The regular ingestion of soil and ant soil of *Atta* sp. by the study group could be how they deal with the toxins in the leaves. In fact, geophagy has been reported for several species of birds: parrots, pigeons, cracids, grouse (Diamond et al. 1999). Soil ingestion might help grind ingested food, absorb plant toxins, acquire essential minerals, and buffer acidic or alkaline foods (Diamond et al. 1999). Detailed analyses of digestive physiology of this curassow are needed to test the various roles suggested for soil consumption.

The phenology of the plants in the study area in 1990–1991 (Stevenson et al. 1998) indicates that fruit production varies seasonally, peaking in April and reaching its lowest abundance in November. The two feeding behaviors used by the study group appear to be related to the pattern of fruit availability. During the period of fruit abundance (January–May), when there was a high diversity of potential foods, the group moved over a large area and hence incorporated a large variety into its diet. By contrast, the group moved little during the period of low fruit supply (September–December). When food was scarce, the cracids would exhibit a conservative strategy by moving less and concentrate their foraging around a guaranteed source of food.

Frugivorous vertebrates (especially birds, bats, and primates) are believed to play a central role as seed dispersers in the natural regeneration of tropical forests (Estrada and Coates-Estrada 1986, Willson et al. 1989, Julliot 1997). Cracids may be important in tropical forests dynamics, not just as seed dispersers but also through seed predation (Érard and Sabatier 1986, Strahl et al. 1997). Repeated foraging in the same patch for fruits, seeds, and cotyledons would diminish the concentration of seeds and seedlings under those trees and affect the distribution of those species.

Although *Ficus* species have been reported to be important for frugivorous vertebrates in some lowland tropical forests (Leighton and Leighton 1983, Terborgh 1986b), they do not appear to be important to *Mitu salvini,* at least in our area. *Ficus* fruits were consumed rarely and opportunistically by the study group. Fruits of other tree species were intensely exploited (e.g., *Guarea guidonia*) and may serve as the primary food for this cracid as well as other non-passeriform birds during the period of food scarcity.

Few field data on natural populations of cracids have been collected; hence, basic information on which to base effective management plans for these birds is still missing (Brooks and Strahl 2000). Some researchers (Silva and Strahl 1991, Borges 1999) suggest that hunting may have a greater impact on cracid populations than habitat degradation but we still do not know. The survival of this commonly hunted species is threatened in the Neotropics (Brooks and Strahl 2000). As a result, there may be little opportunity to assess how cracids use these habitats and influence community dynamics. In the case of Salvin's Curassow, its future seems uncertain at least in the study area as human colonization advances rapidly bringing with it hunting and habitat degradation.

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REPRODUCTIVE ECOLOGY OF THE MAUI PARROTBILL

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AND JAMES R. KOWALSKY[1,3]

ABSTRACT.—The endangered Maui Parrotbill (*Pseudonestor xanthophrys*) is an excavating, insectivorous Hawaiian honeycreeper endemic to the high elevation rain forests of east Maui, Hawaii. From March 1994 to June 1997, we studied various aspects of their breeding ecology. We color-banded 18 individuals, located and monitored 9 active nests, and took behavioral data during 440 hrs of nest observation. Both members of a pair maintained a year-round, all-purpose territory that included nest sites and food resources. Maui Parrotbill were monogamous within and between years; we found no evidence of polyandry, polygyny, or helpers at the nest. Nests were cup-shaped, composed mainly of lichen interlaced with small twigs, and positioned in the outer canopy forks of mature ohia (*Metrosideros polymorpha*) trees. Modal clutch size was one. Females performed most nest construction and all incubation and brooding; males provisioned females and assisted in feeding nestlings after their fourth day. Fledglings depended on parental care for 5–8 months, during which their bill strength increased and foraging skills improved. We calculated the overall nest success rate by the Mayfield Method as 0.42 for the 1995/1996 and 1996/1997 breeding seasons combined. Nest failure and fledgling disappearance coincided with events of high rainfall. Their breeding ecology most closely resembled the Akiapolaau (*Hemignathus munroi*), another excavating, insectivorous Hawaiian honeycreeper found on Hawaii Island. As with the Akiapolaau, the threat of extinction is persistent and results from both the constraints of inherent life history traits and artificial ecological changes. We advocate the protection and expansion of habitable forest areas and an ongoing program to monitor and mitigate the effects of invasive species. *Received 3 Feb. 2000, accepted 23 June 2000.*

The Maui Parrotbill (*Pseudonestor xanthophrys*) is an endangered Hawaiian honeycreeper (Fringillidae: Drepanidinae) and the sole member of its genus. Its range is now limited to the high elevation (>1200 m) forests on the northern and eastern slopes of Haleakala, a dormant volcano which constitutes east Maui Island. Maui Parrotbills are primarily insectivorous, biting open fruit, soft stems, and decaying wood to extract hidden invertebrates (Perkins 1903).

Prior to the arrival of the first Polynesian colonists around 400 AD, the Maui Parrotbill probably occurred throughout much of Maui, Molokai, and Lanai islands and inhabited a diverse assemblage of forest environments from sea level to treeline, as inferred from subfossil evidence and its historic distribution (Olson and James 1982a). During the period of human settlement, expanding agriculture and harvesting of wood products destroyed most of the habitat of the Maui Parrotbill (Olson and James 1982b, Scott et al. 1986). Human colonization also brought alien plants and animals, most notably two mammalian predators of birds, the feral cat (*Felis catus*) and rats (*Rattus* spp.). The introduction of mosquitoes, and, later, alien birds, put in place the building blocks of an avian malaria (*Plasmodium relictum*) epidemic, to which the endemic species had little or no resistance (Atkinson et al. 1995). By the mid- to late 1800s, the Maui Parrotbill was considered rare and highly localized (Perkins 1903). In 1980, the comprehensive Hawaii Forest Bird Survey mapped the species' geographic range at approximately 50 km^2 (Fig. 1; Mountainspring 1987) and estimated the population at 500 ± 230 individuals (95% C. I.; Scott et al. 1986). Early behavioral studies of the Maui Parrotbill focused primarily on foraging ecology (Carothers et al. 1983, Mountainspring 1987). The first two active nests were discovered by Lockwood and coworkers (1994), who described many important aspects of parrotbill breeding biology.

Our study focused on documenting the life history and nesting success of Maui Parrotbills with the aim of assessing factors limiting the population of this endangered species. In

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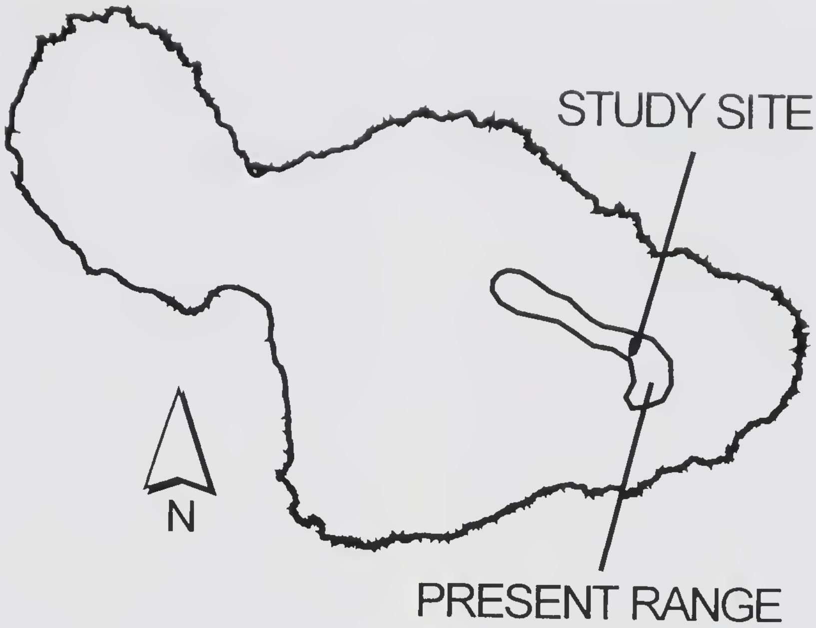

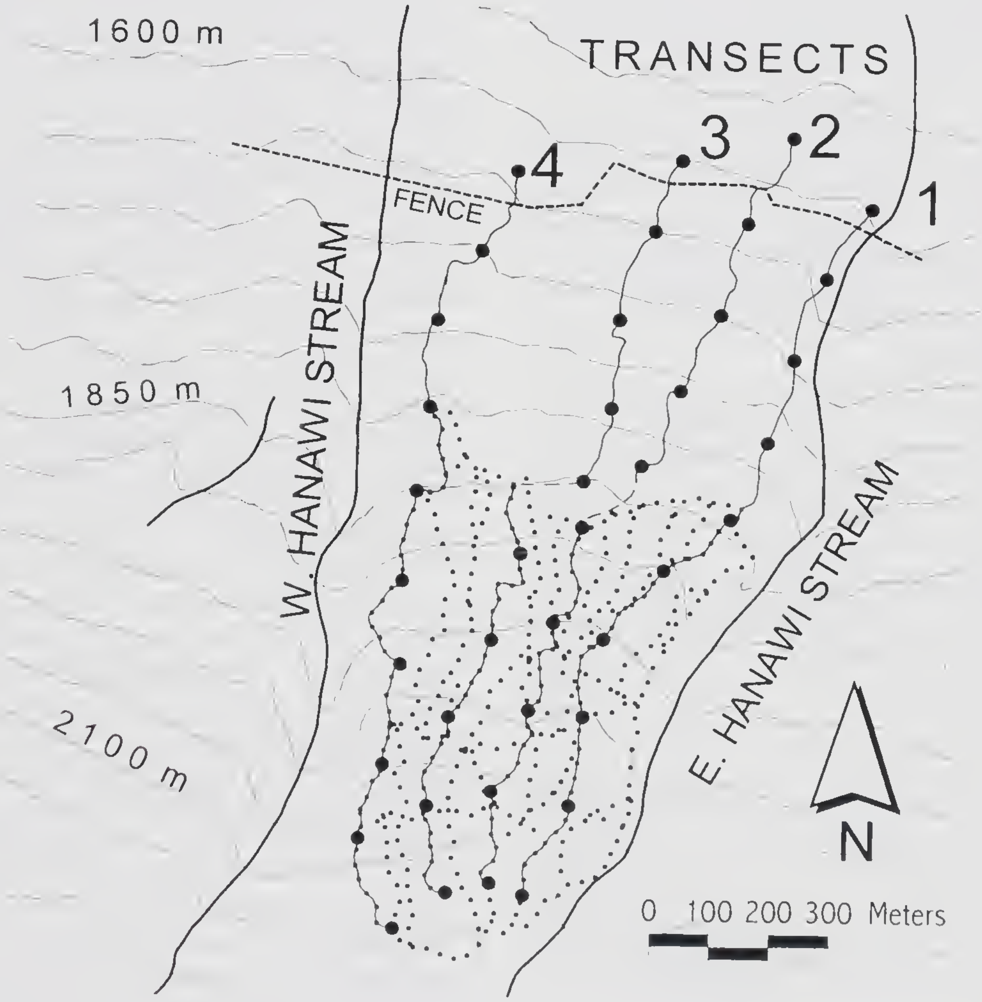

FIG. 1. Study site and location on the island of Maui, Hawaii. Reference flags (small dots) above 1850 m follow trails of main study area. Contour interval = 50 m.

this paper, we expand upon the observations of Lockwood and coworkers (1994) with a more thorough look at Maui Parrotbill courtship, breeding system, nesting behavior, parental roles, and reproductive productivity during three consecutive years of field study.

STUDY AREA AND METHODS

Our 35-ha study site was located on east Maui's northern (windward) slope (20° 45′ N, 156° 08′ W). It was bounded by the east and west branches of the upper Hanawi Stream, approximately 1800–2125 m elevation (Fig. 1) and was the location of Mountainspring's Hanawi study area (1987) and Lockwood and coworkers' site #2 (1994). The topography was rugged, steeply sloped (20–30°), and dissected by numerous ridges and drainage gulches up to 15 m deep. The area was dominated by a wet ohia (*Metrosideros polymorpha*) forest to approximately 2000 m, transitioning above to a narrow band of mesic ohia and subalpine scrub and then into alpine grassland. Other canopy trees included olapa (*Cheirodendron trigynum*) and hoawa (*Pittosporum confertiflorum*). The dense understory included small trees, shrubs, ferns, abundant epiphytes, and few vines (Henrickson 1971, Jacobi 1989).

Local climate was dominated by prevailing northeast tradewinds and characterized by frequent fog, mist, and rainfall throughout the year. Mean annual rainfall exceeded 5.1 m and was aseasonal and highly variable. Mean monthly temperatures ranged from 9.9–13.4° C. Winter months were cooler with nighttime temperatures often falling below 0° C (T. Giambelluca, unpubl. data).

We conducted our field study from March 1994 through June 1997. Trails were established on ridgetops throughout the study site and allowed nearly continuous visual or auditory coverage of the study area while minimizing soil and groundcover disturbance. We used GPS positioned reference flags, placed along trails at 25 m intervals, to calculate UTM coordinates for all other locations. We determined locations using compass bearings and estimated distances for birds or measured distances for nests. These were later mapped using ArcView GIS software.

We used playback recordings of Maui Parrotbill songs and calls to lure 18 after-hatch-year birds (7 males and 11 females) into mist-nets. (Immature birds were generally non-responsive.) Each captured individual was measured, described, and given a unique combination of one stainless steel U.S. Fish and Wildlife Service numbered band and three wrap-around color bands. Adults were sexed using wing, tarsus, and bill measurements. Males were larger (Simon et al. 1997; Berlin et al., in press). We gathered behavioral data as we encountered both banded and unbanded birds throughout the study area. Once a band combination (or unbanded status) was determined, observers waited approximately 10 seconds (to minimize observer effect) before recording observations including location, foraging behavior and substrate, pursuit flights, courtship behavior, vocalizations, group size, and group interactions.

We searched for nests by following individuals as we encountered them, particularly those exhibiting courtship, nest-building, or provisioning. We attempted to cover all trails throughout the study area equally; however, poor weather sometimes affected our search schedule. When an active nest was located, we marked its position with a PVC spotter (Simon 1998) and departed the area to minimize disturbance. Subsequent nest observations were conducted with the aid of a spotting scope and from a camouflaged blind 10–50 m from the nest tree. We could typically see a viewing range of 1–3 m radius around the nest.

Most observation sessions at nests lasted 2–4 hr ($\bar{x}$ = 3.0, max. = 8.6 hr) between 07:00 and 17:00 HST. We attempted to observe each active nest at least once a day or every other day, weather permitting, and varied the starting times for the sessions at each nest. We assumed that the female was incubating if she spent at least 50% of an observation session sitting on the nest with absences not exceeding 25 minutes. For nests found in the incubation stage, we assumed the nestling period to start when we observed the female feeding nestlings or removing fecal sacs. For analyses of the lengths of incubation and brooding bouts, we used mean bout length for observation sessions lasting at least 1.5 hr. We recorded the arrival and departure of the female, the start and end of incubation and brooding bouts, the number of times the female checked or manipulated the contents of the nest (when possible), and the frequency of female-chick, male-chick, and male-female feedings on or near the nest. We also noted the occurrence of other behavior and intra- and interspecific interactions. When they could be seen, we described the appearance and general behavior of nestlings. When multiple observation sessions were conducted at a nest during a single day, the data for those sessions were pooled.

We defined successful nests as those fledging at least one chick. We took as evidence of success observations of nestlings within 2 days from the expected fledge date or an adult feeding fledged young within 25 m of the nest tree (or farther if the adult was identified by bands). In addition to nest summary statistics, we calculated nest success using the Mayfield Method (Mayfield 1975, Johnson 1979). Exposure days included the first day for which the nest was active, where active was defined as being in the incubation or nestling stage, through to fledging or nest failure. We assumed nest status changed on the midpoint date between checks if no other data were available (Mayfield 1975). Because we could not see newly hatched chicks below the nest rim, we did not attempt to differentiate between success rates for incubation and nestling stages. We determined nest fate by direct observation and/or subsequent collection of the nest. Excluded from the analyses was the only active nest found in the 1996/1997 breeding season; only cursory observations were made in order to facilitate collection of the egg for captive rearing.

Post-active nests and their contents were collected by climbing to them when possible. For collected nests, we measured the nest height above ground with a weighted line; we measured nest height for nests not collected, and tree height with a clinometer. Dimensions of the nests were measured while they were fresh. Collected eggs and nests were deposited at Bishop Museum, Honolulu. We also collected one live egg in 1997 for rearing at the Zoological Society of San Diego's Keauhou facility.

RESULTS

We monitored nine active and five inactive Maui Parrotbill nests over the course of three winter/spring breeding seasons (Table 1). We found an additional nest under construction in each of the first two breeding seasons and three under construction in the third breeding season that did not become active. Four of nine active nests were found during the construction stage, and four more were found early in incubation. We found nest construction as early as 1 November and fledging of young as late as 28 June. One nest attended by a female was found in October 1997 after the field study ended. Pairs may renest up to two times after failure; however, we found no evidence of renesting following successful fledging within a season.

Breeding system.—We accumulated 766 observations of unbanded (n = 497) and banded (n = 269) birds away from nests. Courtship behavior was observed on five occasions from November through April and included singing by the male, wing-flutter displays by both male and female, and males presenting small twigs or leaves to the female. Females also solicited regurgitate from males. Evidence from two banded pairs of Maui Parrotbill suggests that the species is monogamous both within and between years. Members of one banded pair remained together for three years of the study, and members of another banded pair remained together for two years before the study ended. Although we found no nests for the first pair, we observed them attending fledglings in two years. We observed no evidence of helpers at any nest (n = 9; Table 1).

Based on resighting locations for banded birds, we observed that each breeding pair with at least one member banded (n = 6)

TABLE 1. Summary of Maui Parrotbill nest activity, 1995–1997.

Breeding pair	Banded?		Breeding season	Nest attempt	Start of incubation	Successful?/Stage at termination	Notes
	Female	Male					
1	WWWA	NO	94/95	1	2/8/95	N/Egg	Failure associated with poor weather.
1	WWWA	NO	94/95	2	3/20/95	N/Nestling	Nest empty; failure assoc. with poor weather.
2	NO	NO	94/95	1	4/8/95	N/Egg	Failure associated with poor weather.
3	(BABR)	NO	94/95	1	5/23/95	Y	Fledged 1. (♀ banded after breeding season.)
3	BABR	NO	95/96	2	4/24/96	Y	Fledged 1. First nest in 1996 season not active.
4	GAGB	ABGR	95/96	1	12/23/95	Y	Fledged 1. Fledgling presumed lost; assoc. with poor weather.
4	GAGB	ABGR	95/96	2	2/96	N/Egg	Start of incubation unknown. Abandoned in incubation stage; associated with poor weather. Seen later in season with 1 Fledgling.
4	GAGB	ABGR	96/97	1	1/97	Egg	Egg collected for rearing
5	GAGG	NO	95/96	1	1/15/96	Y	Fledged 1. Young possibly lost within 1 week of fledging; not seen after extended rainfall.

maintained a relatively stationary, year-round home range. Because adjacent home ranges had minimal overlap and males exhibited both counter-singing and agonistic chase behavior throughout much of their home range, we suggest that a defended territory overlies most of the home range area.

Nest construction.—All nests were a basic cup design and located in canopy forks just below the outer canopy of mature ohia trees. Nest heights above ground level, measured for eight active nests and one inactive nest, averaged 11.6 m [±3.0 (SD), range 8.7–18.3], and the height of the nest trees averaged 13.4 m (±3.1, range 9.5–18.8). Nest construction was performed primarily by the female. The two males we observed carrying nesting material to nests did so early in construction, suggesting that males might play a role in nest site selection. All nests were composed primarily of lichen (*Usnea* sp.) with small (<2 mm diameter) defoliate pukiawe (*Styphelia tameiameiae*) twigs interspersed throughout. We did not observe the initial attachment stage of nest building. Middle to late construction consisted mainly of adding material to the inside of the nest cup and using legs, belly, and breast to integrate it into the overall nest structure. Four nests contained fine strips of fern root fibers as cup lining; one contained thread-like strips of inner bark material, probably olapa. We estimated nest construction to be 7–18 days. Light rainfall did not appear to impede work on the nest, but heavy rains or high winds slowed or delayed building activity.

Eggs.—Maui Parrotbill eggs were ovate with an off-white to tan base color and lavender brown mottling concentrated on the rounded half, decreasing near the apex. Six eggs averaged 21.7 mm long (range 20.6–22.9) and 15.4 mm wide (range 14.6–16.5; our data plus unpubl. data from the Zoological Society of San Diego from eggs collected after our study and from within 5 km of our study site). We found clutches of one egg only. All successful nests fledged single young and nests that we collected containing eggs held a single egg.

Nest attendance.—At seven of nine active nests with at least one adult banded, incubation and brooding was performed exclusively by the female. We estimated the incubation period to be 16 days from a single nest we followed from construction to the nestling stage. We accumulated a total of 126.5 hours of nest observation at six nests during incubation and found that females spent an average of 75.3% of daylight hours on the nest. The balance of their time was typically spent foraging away from the nest tree or soliciting feedings from the male with soft *chew* calls and wing-flutter begging displays. Males provisioned the females almost exclusively by regurgitation and averaged 0.31 feedings/hr. Because many feedings took place off the nest and out of our observation area, actual provisioning rates were likely higher.

We followed one nest from late incubation to fledging and found the nestling stage to last approximately 20 days. Observations on four nests with nestlings totaled 214.2 hours. During the first 3–4 days, the female's brooding times were comparable to those at incubation, and the male provisioned the female exclusively, with the female periodically regurgitating smaller boluses to the hatchling. Feedings during this stage were not clearly visible to observers; therefore rates could not be accurately determined. The adults removed the fecal sacs of young nestlings (1–9 days old); afterwards, nestlings defecated over the nest rim and occasionally on it.

Older nestlings were fed by both adults at a rate of 1.8 feedings/hr. As the chick grew, the female spent more time away from the nest area, typically brooding during the day only during periods of rain or cold. Nestlings remained alert throughout the day and spent much of their time preening.

Fledglings.—Fledglings left the nest quickly, typically spending less than 1 day in the vicinity of the nest before permanently departing the nest tree. Newly fledged young were moderately strong flyers but usually stayed quiet and immobile in mid- to upper canopy foliage. Adults, most often the male during the first 7–10 days, sought out fledglings for feedings. Young Maui Parrotbill remained with their parents 5–8 months after fledging (*n* = 2). During this period, young were frequently observed following foraging adults and soliciting feedings (79% of all juvenile-adult sightings; *n* = 75). These juveniles persistently emitted a *chew* begging call at 1–2 sec intervals.

Young left the nest with bills not fully developed in size or rigidity. General observations of fledgling and immature Maui Parrotbills suggested that foraging behavior developed gradually. Initially, they showed no signs of feeding themselves. Foraging began first as leaf and twig gleaning and then over the course of several months transitioned to lifting epiphytes, probing decaying wood and soft fruits, and, finally, to splitting stems and other harder vegetative matter. Only when the next nesting season began did adults chase young from the breeding territories.

We obtained little information on the dispersal patterns of Maui Parrotbill young. One subadult female parrotbill banded 2.5 km east of our study site appeared at our site 44 days later in association with a banded resident male who had not bred that year. The occasional association of immature individuals with nesting pairs suggests that young may stay at the periphery of their parents' territory until the end of their first year.

Nest success.—Nest success rates (successful nests divided by active nests with known fate) for the 1994/1995 and 1995/1996 breeding seasons were 25% and 75%, respectively for all four nests in each breeding season. Mayfield estimates of the overall success rate averaged 0.42 (166 exposure days). With the exception of one nest that failed because the egg was probably infertile, unsuccessful nests and the disappearance of a single fledgling banded in the nest occurred during the heaviest rainfalls in the nesting season. We found no evidence of nest depredation. However, two active nests that failed contained no eggs or nestlings when collected and possibly were depredated.

It was difficult to find all nests for each pair because few home ranges lay entirely within the boundaries of our study area. One banded pair, whose home range was only partially within the study area and for whom we did not find nests, was observed with young in both the 1994/1995 and 1995/1996 breeding seasons. An empty nest without fecal material on the rim was found in this pair's territory late in the 1996/1997 breeding season, suggesting that they bred unsuccessfully that year. In 1995/1996, the only other banded pair lost one fledgling during an extended period of heavy rain, abandoned a second nest in heavy rain during incubation, but was seen later in the season with a fledgling. Other pairs, too, may have had a nest fail in our study area and have had a later, successful nest outside it.

DISCUSSION

Our research confirmed that Maui Parrotbill have an extended breeding season, November through June, as surmised by Mountainspring (1987). As a result of this long breeding season and the extended period of juvenile dependency, parents with young can be found throughout the year. The nesting period overlaps that of sympatric, nectarivorous honeycreepers (Berlin and VanGelder 1999). However, it is longer and begins earlier than that of the insectivorous Maui Alauahio (*Paroreomyza montana*; H. Baker and P. Baker, pers. comm.). Because heavy rainfalls that disrupt nesting are seasonally unpredictable, parrotbills cannot avoid them by seasonal breeding. Instead, nesting phenology may correspond to an annual increase in prey biomass and/or a decrease in the cost of capturing them.

In the Hanawi study area, Maui Parrotbill showed a uniform pattern of nest construction and placement. In other parts of their range, Maui Parrotbill have been known to utilize other nesting materials. To the east of our study site, where *Usnea* lichen is less abundant or absent, nests may be constructed with epiphytic mosses including *Thuidium plicatum, Macromitrium microstomum,* and *Floribundaria floribunda* (*n* = 2; P. Baker, H. Baker, and W. Hoe, pers. comm.). Nest placement may vary with habitat. Maui Parrotbill formerly showed a close association with koa (*Acacia koa*) forests; Perkins (1903) found a nest typical of the Maui Parrotbill in a koa. Whatever the substrate, the placement of nests in the outermost layer of the canopy may limit nest depredation by introduced mammalian predators, particularly rats. The only confirmed nest depredation by rats during our larger study was that of an Akohekohe (*Palmeria dolei*) female and eggs in a nest that was atypically low in a tree and close to the main stem (Pacific Island Ecosystems Research Center, unpubl. data).

Weather had a substantial effect on nest success and the survival of dependent young. Exposure might kill eggs, nestlings, or fledglings and might drive females from their nests or limit foraging. Although our observations were curtailed during inclement conditions, we noted that Maui Parrotbill appeared to spend less time foraging during periods of moderate or heavy rainfall. Rain and wind might significantly reduce the visual and auditory cues used to detect large, energy-rich borer larvae and might reduce foraging success.

Nesting pairs in our study never raised more than a single young in any given season. The Maui Parrotbill has been known to successfully hatch 2 egg clutches, based on observations of adult pairs with two dependent young; however, such sightings have been rare (less than 5 cases out of at least 40 parent/juvenile groups; this study, P. Baker and H. Baker, pers. comm.). No data are available on the percentage of young that reach independence from 1 or 2 young clutches or broods. Information on the recruitment rate for this species was, and will continue to be, difficult to acquire.

Some of our findings have implications for Maui Parrotbill systematics. We found marked differences between the breeding biology of Maui Parrotbill and sympatric nectarivores, such as the Hawaii Amakihi (*Hemignathus virens*), and the only sympatric insectivore, the Maui Alauahio (Table 2). Parrotbills also differed from the finch-billed honeycreepers with which they have traditionally been classified (Table 2; Berger 1981, Pyle 1997). On the other hand, the maintenance of large territories, one-egg clutches, and exceptionally long juvenile dependency period show that Maui Parrotbill share more features of their life history with the Akiapolaau (*Hemignathus munroi*) an insect excavator found on Hawaii Island. Perkins (1903) allied the two species, and recent DNA evidence indicates that they are sister taxa among the living Hawaiian honeycreepers (R. Fleischer, pers. comm.).

The future of the Maui Parrotbill remains very much in question. This honeycreeper is now confined to the wettest and highest portion of its original range. This habitat may be marginal, as indicated by the loss of eggs, nestlings, and fledglings to heavy, but not atypical, rainfall. Koa trees, strongly favored by the Maui Parrotbill as a foraging substrate (Perkins 1903), are rare and patchy above 1200 m elevation, and efforts to re-establish koa forests have so far been minimal. Trans-

TABLE 2. Comparison of select life history traits. See footnotes for scientific names and source references.

Common name	Palila[a]	Laysan Finch[b]	Maui Parrotbill[c]	Akiapolaau[d]	Maui Alauahio[e]	Hawaii Amakihi[f]
Primary food types	Green seeds/ Insects	Omnivorous	Insects (Excavator)	Insects (Excavator)	Insects (Gleaner)	Nectar/ Insects
Year-round, all purpose territory/Breeding territory	N/N	N/N	Y/Y	Y/Y	Y/Y	N/Y
Typical clutch size	2	3	1	1	2	2–3
Mean incubation/Nestling period (days)	17/26	16/24	16/20	?/21	16/18	14/17
Juvenile (dependence) period	<1 mo.	~1 mo.	5+ mo.	4–5+ mo.	18–20	<1 mo.
Maximum number of broods/year	2	2	1	1	1	2

[a] *Loxioides bailleui*; Pletschet and Kelly (1990), Pratt et al. (1997).
[b] *Telespiza cantans*; Morin 1992.
[c] *Pseudonestor xanthrophrys*; this study, Simon et al. (1997).
[d] *Hemignathus munroi*: Ralph and Fancy (1996), Pacific Island Ecosystems Research Center, unpubl. data.
[e] *Paroreomyza montana*; H. Baker and P. Baker, pers. comm.
[f] *Hemignathus virens virens* (Hawaii Is. ssp.): van Riper (1987).

location of individuals into lower elevation areas within their former range would not be expected to be successful because of the high probability of mortality from avian malaria.

Inherent life history traits, such as large home range, apparent high site fidelity, extended juvenile dependency, and low productivity presumably slow population growth for the Maui Parrotbill. Coupled with a restricted geographic range and low abundance, these traits may also limit the species' ability to recover from severe weather events or from the advent of new threats. If this fascinating species is to survive beyond the immediate future, every effort must be taken to protect, restore, and expand upper elevation ohia/koa forests, and to consistently assess and respond to potential threats posed by non-endemic flora and fauna.

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INFORMATION ABOUT BEHAVIOR IS PROVIDED BY SONGS OF THE STRIPED CUCKOO

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ABSTRACT.—Striped Cuckoos (*Tapera naevia*) have three different song types. We investigated behavioral correlates of two using interactive playback to simulate territorial intrusion. Individuals sang one song type frequently when not interacting closely with neighbors, mates, or playback. A less common song type was sung by subjects that had approached playback closely, and by closely countersinging neighbors. These two song types distinguish different extents to which a singer may take initiative leading to interaction: the first provides information that the singer will probably stay put and not interact closely unless approached, the second that the singer will itself approach and search for another individual. Such distinctions are significant because they parallel recent results from diverse passerines, and because the information may be fundamental in enabling singers to obviate or elicit encounters with distant individuals. *Received 6 July 1998, accepted 10 June 2000.*

Diverse animals at times signal in sequentially ordered, near-rhythmic bouts termed singing (Smith 1991), the structural properties of which transcend major phylogenetic boundaries. What singing offers may be information that is especially important to individuals when out of each other's sight.

Information refers here to any property of objects or events that facilitates predictions about them (Smith 1997). Information thus reduces uncertainty. Even markedly different kinds of animals have common informational needs. For instance, animals often must monitor each other's locations and activities. Songs (the main components of singing performances) help by providing some information about identity (Becker 1982, Falls 1982, Nelson 1988) and location (Wiley and Richards 1982, Naguib 1995). Additional information contained within a song includes aspects of a singer's behavior and can influence the likelihood of close interactions. Despite its significance, such information has received little attention (see partial reviews by Dabelsteen 1985; Smith 1977a, 1991; Spector 1992).

When a bird matches a song type uttered by a neighbor, it provides information concerning both its attentiveness to that neighbor and its readiness to interact. However, individuals of many species do not match songs. Instead, they select among different song types and variants, making available information about the extent to which they will take initiative in interacting. Most simply, a singer indicates the probability that it will either actively seek out and approach other individuals or remain where it is, responsive but leaving further initiative to others. Such information should help mates, neighbors, or strangers decide whether to interact closely with a singer, negotiate (see Discussion), or remain apart and accept the singer's current behavior.

We make no inferences about the extent to which songs' information enables reliable prediction (is "honest"). Our interpretations are empirical, based on what we see singers do when uttering different songs. Once known, the same types of behavior that correlate with a vocalization when the singer is visible can be expected to occur even when the signaler is unseen. The same information is also available to listening birds. If signaling is deceitful, the correlations break down.

We used playbacks and observations of behavioral responses to ask whether the widely shared structural and functional properties of singing provide types of information that are fundamentally similar among oscine, suboscine, and nonpasserine birds. Our goal—unusual for playback experiments—was not to compare effects of different stimuli but to affect subjects' behaviors. We asked what they sang in conjunction with specific behaviors. A song type correlated with a specific behavior could inform listeners that a singer is engaged in that behavior. We used playbacks to elicit behavior that is difficult to observe in actual disputes. We compared behavioral informa-

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TABLE 1. Playback stimuli and the kinds of vocalizations uttered by each subject before playback and in its initial singing when close to playback.

	Playback stimulus		Preplayback singing			Initial vocalizations when close	
Subject	*Sem-fim*	*Wee*	*Sem-fim*	*Wee*	Silent	Brief tones	*Wee*
1	1		X			X	X
2	1		X			X	X
3	1		X			X	X
4	2		X			X	X
5	2		X			X	X
6	2		X			X	X
7	3		X			X	X
8	3		X			X	X
9	4		X			X	X
10	4			X[a]		X	X
11	4		X			X	X
12	5			X[b]		X	X
13	6				X	?[c]	X
8		1	X			X	X
14		2	X			X	X

[a] Bird #10 was not countersinging before playback, but was apparently with a mate that uttered a *feeee*-series song.

[b] Bird #12 was countersinging with a neighbor before playback began.

[c] Bird #13: recording failed during the first part of this trial. We may have failed to hear faint brief tones in the field.

tion provided by songs of the nonpasserine Striped Cuckoo *(Tapera naevia)* with that made available by songs of passerines studied previously (Smith 1988; Smith and Smith 1992, 1996a, b).

The cuckoo is a resident of scrubby pastures, llanos, and cerrados from Mexico to Argentina. Individuals often sing from bushtops and even trees, but are otherwise inconspicuous. They forage amid vegetation, primarily on or near the ground and readily run (Howell and Webb 1995). Each of their three song types has a distinctive behavioral correlate.

METHODS

Field work was done from 1–9 July 1989 and 28 May–13 June 1992 on Hato Piñero, a ranch and nature preserve of 26,000 ha in the llanos of Cojedes, Venezuela. Each of the 14 unmarked experimental subjects was on a separate site. We made additional notes on another eight individuals that were not involved in experiments.

Our observations and an account by Sick (1953) led us to predict that at least two of the three different song types (termed *sem-fim* and *wee*-series) would be uttered in conjunction with distinctive interactional behaviors. Our tests involved simulating spatial intrusions to elicit approach and search. Search was operationally defined as conspicuous scanning movements, often involving perch changes. We compared vocalizations uttered in conjunction with approach and search behavior to pre-playback samples of 5–50 songs and post-playback samples of 2–5 min/bird.

Our playback was interactive. We adjusted it within preset limits to the behavior of each subject as a trial developed because each subject had its own experiences and temperament and responded uniquely. Presumably, subjects did not expect to encounter an intruder that did not interact but repeated songs on an irrelevant schedule. Our interactive trials therefore differed from one another in details that inevitably differ in natural encounters.

Our procedures were one of two types of interactive playback. One uses a fixed speaker position and predetermined rules to alter the stimuli that are played back (Dabelsteen and Pedersen 1990, Dabelsteen and McGregor 1992). Instead, we interacted by adjusting the timing of playback of a single type of stimulus relative to each subject's actions. This allowed us to accommodate to the subject's rate of approach and vocalization and to move the playback speaker to simulate an elusive intruder's probing, evasive movements (Smith 1988, 1997; Smith and Smith 1992, 1996a, b).

Each subject was located by its loud singing. We began recording when we had approached to 50–100 m from the bird, and continued until the subject approached to within 20 m. For four subjects that did not approach promptly we interrupted playback and moved to a nearby location one to three times (not more than once per min). One of us kept the speaker facing the subject and in vegetation that could conceal an intruder to provide the subjects a site to search. Each subject was used once, except subject 8 (Table 1); it first heard *sem-fim* playback and then *wee*-series playback. No subject heard the playback of a neighbor's song.

Continuous playback of *sem-fim* to nine subjects contained 5 s natural silent intervals between songs.

Four other subjects sang rapidly and continuously, and we played back single *sem-fim* songs in answer to every second, third, or fourth of their songs. We stopped playing a song when a subject closely approached the speaker. However, for six subjects that became silent after approach, we eventually played single songs or brief bouts of *sem-fim* faintly from one to three nearby sites. *Wee*-series songs were played back to only two subjects. Recording continued until all but one subject had reverted to *sem-fim* singing or become silent.

We used a Sony TC-D5M stereo cassette recorder and an electret microphone (Radio Shack 33–1060) on a Sony PBR-330 parabola. Behavioral notes were dictated onto the parallel recording track. Playback was from a Sony CFS-W50 recorder with a 1 watt speaker, adjusted to sound as loud as a cuckoo singing 35 m away (corresponding to an SPL of 75–82 db, 1 m from the speaker). Playback to the six subjects that initially kept silent after approaching was at 58–62 db, simulating the faintness with which other subjects first responded when close.

Playback stimuli were previously recorded songs, each from a different individual. We lacked sufficient subjects and time to complete controls with *wee*-series stimuli, partly because four *sem-fim* stimuli were each played to more than one subject (Table 1) to obtain at least one well recorded trial with each stimulus. (We could not, in the field, adequately assess faint vocalizations.)

Vocalizations were analyzed on a Kay Elemetrics DSP-5500 sound station, using a transform size of 100 points (150 Hz) on a 0–4 kHz frequency range and the Hamming windowing function. Significance was evaluated by the two-tailed sign test (Siegel 1956).

RESULTS

Fourteen subjects approached the playback speaker and sang. Most came within 10–20 m and progressed consistently through two song types and several different faint tones while performing several visible displays. A third song type was recorded but not during approaches.

Vocalizations.—The most common song was a clear, rising couplet (Fig. 1A). The Brazilian name for the bird, *sem-fim,* means "without end", apt for a song that is sometimes repeated all day and all night (Sick 1953). Slight variation in frequency and duration was common, but abrupt frequency shifts, broken components, and greatly shortened inter-component intervals were rare. Nearly all *sem-fim* songs were monotonously alike.

A less common song had an ascending series of usually 4–7 (range: 1–16) *wee* components, with each component increasing slightly in frequency and amplitude. Inter-component intervals were briefer than in most *sem-fim* songs. Most of an individual's simple *wee*-series songs began lower than its *sem-fim* but finished at least as high (Fig. 1B). "Elaborated" *wee*-series songs terminated with a flat or descending component of lower frequency (Fig. 1C).

The rarest song type was a series of gently rising, 0.3–0.5 s components, arbitrarily termed *feeee* (the audible distinction between *feeee* and *wee* is not fit by our alphabet). Figure 1D shows a *feeee* song of three components being answered by another individual's couplet of elaborated *wee*-series songs. Most of the 37 recorded *feeee*-series songs had two to four components. Simple and elaborated forms occurred, as in *wee*-series songs.

Hardest to characterize were extremely faint, brief tones (Fig. 2). We heard these only when within 10–15 m of a subject. The parabola mounted microphone detected many cases we did not hear in the field, but may have missed others. Consequently, we made no statistical analyses of their occurrence.

Such tones were variable and many resembled abbreviated components of songs, condensed songs, or fragmented songs (Fig. 2A, B); most resembled *wee* more than *sem-fim.* One subject divided components of *wee*-series songs into brief segments (Fig. 2C), each indistinguishable from the briefest tones of other individuals. Overall, brief tones comprised few of the recorded vocalizations and had narrowly defined uses (see below).

Visible display behavior.—Cuckoos that approached the playback and sang alternately raised and lowered their crests up to once per second, often rhythmically although not synchronized with their singing. Crest raising sometimes continued for several minutes. The birds' bodies were usually hunched and their wings held slightly out and down with the dark alulas extended. Back feathers appeared ruffled in some subjects. Tails were usually fanned, although rarely widely. Individuals facing the playback speaker swayed from side-to-side without pivoting.

Vocal behavior with approach.—After closely approaching playback of *sem-fim,* all 13 subjects uttered bouts of *wee*-series songs (Table 1). None uttered any *sem-fim* until much later. We avoided pseudoreplication (see

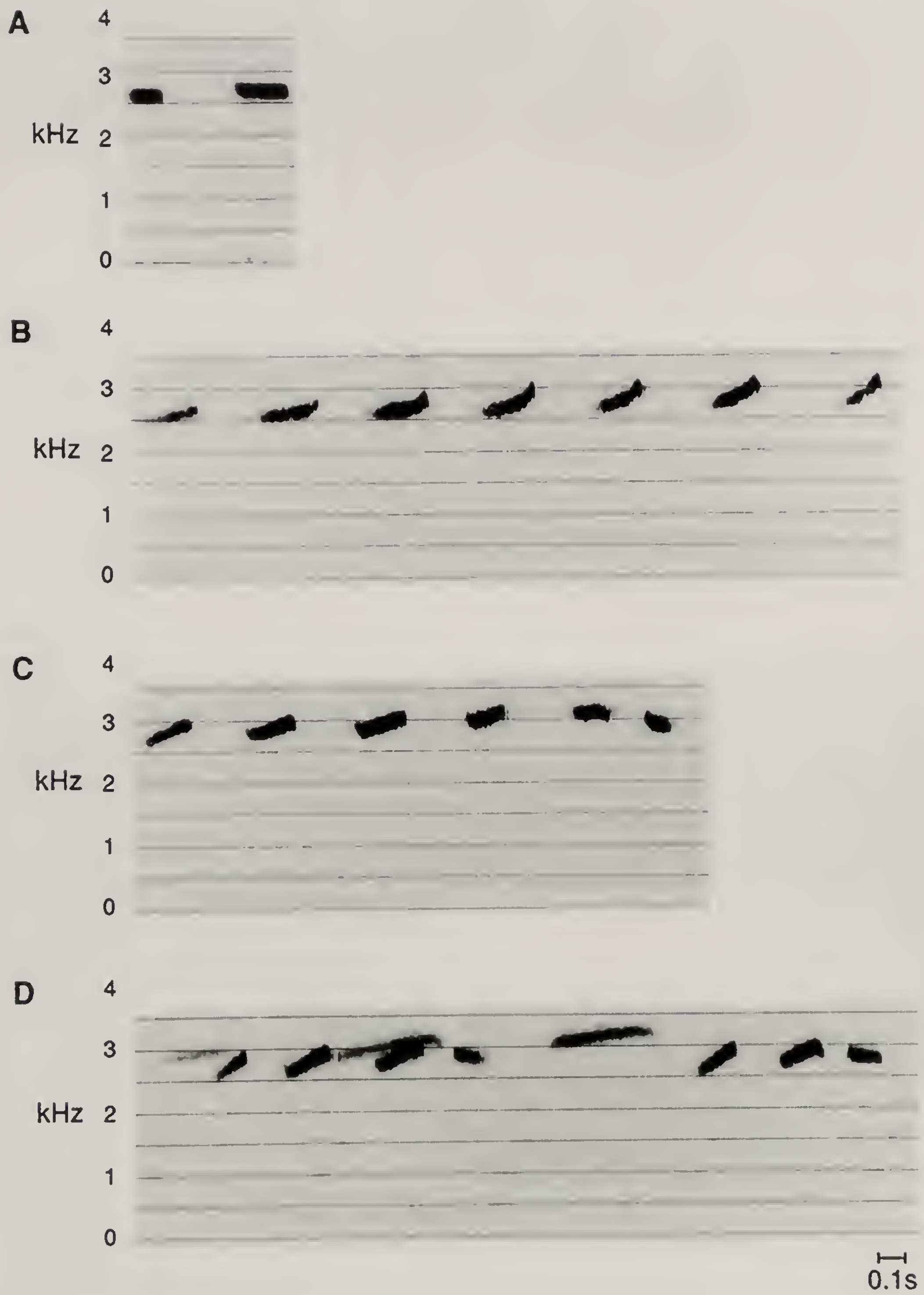

FIG 1. Examples of songs from four different individuals. (A) *sem-fim,* (B) simple *wee*-series song, (C) elaborated *wee*-series song, (D) a *feeee*-series song of three components, overlapping the first *wee*-series of a couplet of *wee*-series songs by a nearby individual.

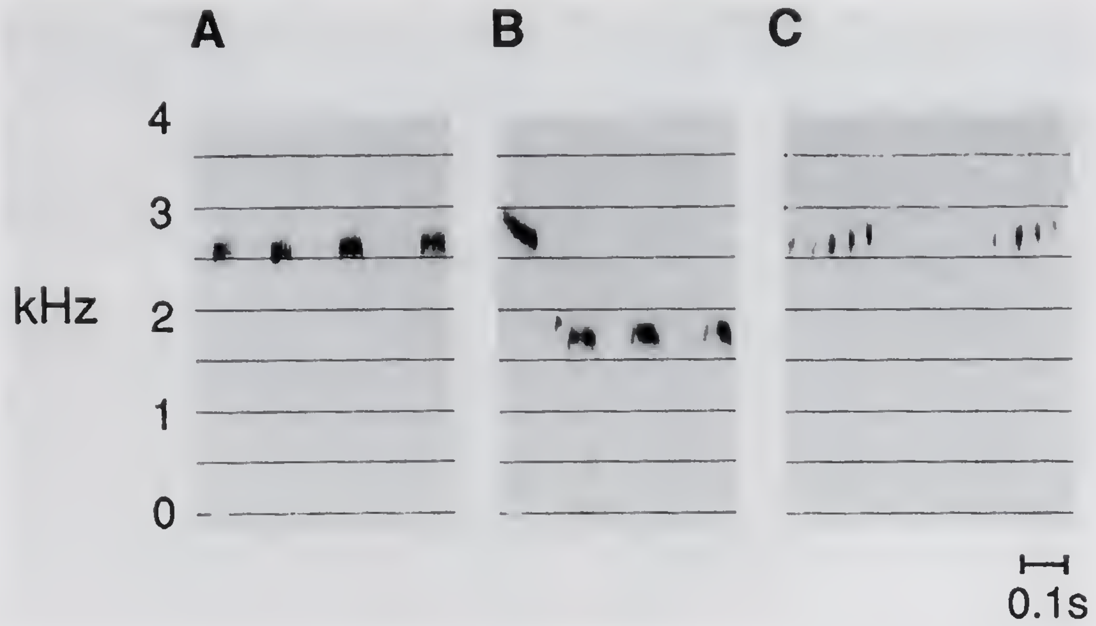

FIG 2. Examples of brief, variable tones (A) and (B) from one individual, (C) from another.

Kroodsma 1989) by using playback stimuli recorded from six different subjects (Sign test: $P = 0.03$).

One subject heard only *wee*-series playback. Like the others, it approached and sang *wee*-series songs. We also played *wee*-series to 1 of the initial 13 subjects after it had approached *sem-fim* playback and begun *wee*-series singing; it continued its *wee*-series. We returned 40 min later, long after it had reverted to *sem-fim* singing, and played that same *wee*-series stimulus. It again approached, singing long *wee*-series. Neither it nor the last bird sang elaborated *wee*-series.

After we stopped playback, nine subjects eventually changed to *sem-fim* bouts. Four others became silent. We ceased recording the remaining subject before it changed.

After approaching the playback speaker closely, a subject typically progressed from silence to brief, variable vocalizations, then to a bout of lengthening *wee*-series. When the speaker was moved and a subject made successive approaches, long *wee*-series songs came more quickly after each move, although the first song after an approach flight was rarely the longest. Four subjects shifted from long simple to long elaborated *wee*-series songs.

Brief tones occurred only in transitional phases. At least 11 subjects approached the speaker silently and eventually uttered such brief tones before bouts of *wee*-series songs. At least four subjects uttered brief tones as they reverted to *sem-fim* singing.

Only two subjects vocalized during approach movements. Neither was close to the speaker. One uttered shortened vocalizations and condensed variants of short *wee*-series songs during two flights and two runs. The other uttered an 8 component *wee*-series song while running along a branch, then came no closer.

The only individual to utter *feeee* during trials was a bird close to our subject, perhaps its mate. It sang once and was overlapped by a *wee*-series song of the subject before the subject approached the speaker.

Bouts of *sem-fim* were heard from eight individuals in addition to our experimental subjects. Prevalence of *sem-fim* songs is consistent with the evidence from preplayback samples: 11 of 13 subjects that were vocal before playback were singing *sem-fim*. The two exceptions were singing *wee*-series in the predawn chorus, when *wee*-series songs are common. *Sem-fim* was the most commonly uttered song type (Table 1) of birds that were not interacting closely.

Twice our playbacks resulted in neighbors approaching within 40 m of each other. They countersang *wee*-series songs and continued singing long after we ceased playback. We saw no close spontaneous encounters. Distant but audible neighbors all sang *sem-fim*.

Five individuals sang *wee*-series songs, primarily in crepuscular periods. Each apparently duetted with another individual that uttered *feeee*-series songs. The *wee*-series singer tended to produce many quick couplets of songs (see Fig. 1D). Couplets were otherwise recorded only from two subjects that did not approach the speaker. Members of each of the five dyads were closely attuned: 36 of the 37 recorded *feeee*-series songs were overlapped by a *wee*-series song. The dyad birds were much closer to each other than *sem-fim* singing neighbors ever were. We played the recorded song, but only one *wee*-series singing individual (mentioned above) approached the speaker. Its unseen companion went silent.

DISCUSSION

The three easily distinguished song types of Striped Cuckoos were associated with the following different activities: individuals that were not otherwise interacting and were not close to neighbors sang long bouts of *sem-fim.* All individuals that countersang against close neighbors or that had closely approached playback, sang *wee*-series songs. *Feeee*-series songs occurred only in apparent duets. All individuals singing *sem-fim* stopped after closely approaching the speaker. After a period of silence, most uttered faint, brief, marginally detectable vocalizations, then sang increasingly louder *wee*-series songs.

During its initial, faint singing each subject remained perched, often within cover, vocally probing to elicit responses from the simulated, unseen intruder. Faint singing may be a wary negotiating move that is audible only to nearby listeners. Negotiations are continuing exchanges of signals without committing to attack or another behavior as each participant assesses the other in a competitive situation (see Smith 1977b, 1985, 1997; Hinde 1985; Colmenares 1991). Faint vocalizations may not be loud enough to attract the attention of this species' hosts or predators. When near the site of a recent playback, the subjects' *wee*-series songs became louder and longer, then usually changed gradually into loud *sem-fim* singing.

Brief tones were uttered primarily during transitions from silence to *wee*-series when subjects were behaving warily, and less often when subjects reverted from *wee*-series to *sem-fim.* Such subjects had not engaged in active confrontation. Their faint tones correlated with an investigative, probing phase of approach, similar to the *churr* song form of *Myiarchus crinitus* (Smith and Smith 1996a).

In the two close countersinging events, neighbors approached to within 50 m and sang *wee*-series songs. Because none attacked, *wee*-series do not appear to indicate a high probability of immediate escalation from approach to fighting. Furthermore, *wee*-series songs were uttered both in duets (by one participant) and in encounters by opponents. In several tyrannids (*Contopus virens,* Smith 1988; *Tyrannus tyrannus,* Smith and Smith 1992; *Myiarchus crinitus,* Smith and Smith 1996a), the song types used in interactions with neighbors were also used with intruders and mates. Thus, such songs provide information only about the probability of the singer initiating interaction, and not about some specific behavioral subset such as disputing with a neighbor or joining a mate.

The *feeee*-series song was not given in responses to playback. It was uttered by birds that were near *wee*-series singing individuals and may have been mates duetting. Sick (1953) described *feeee* in duets of mates. In our interactive playback studies of many species of tyrannids, furnariids, and tropical parulines, mates have vocalized in response both to playback stimuli and to each other (Smith 1996).

Our studies have now shown that the nonpasserine Striped Cuckoo resembles diverse passerines in having different songs that correlate with different extents to which a singer actively promotes close interaction (i.e., either approaches or stays put, singing, leaving further initiative to other individuals). That singing can provide such information may thus be of fundamental importance when separated individuals must choose whether to interact more closely.

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SEASONAL VARIATION IN NEST PLACEMENT BY THE CALIFORNIA GNATCATCHER

KEITH W. SOCKMAN[1,2]

ABSTRACT.—Nest placement of open-nesting bird species may affect risk of nest predation, nest microclimate, and reproductive success. In populations that breed in multiple habitat types and over long seasons, nest placement should vary seasonally and by habitat to compensate for seasonally changing and habitat specific environmental conditions that might affect the relationship between nest placement and reproductive success. Using data collected during 1994 and 1995, I investigated seasonal and habitat specific patterns of nest placement in a population of California Gnatcatchers (*Polioptila californica*) that breeds over a 5 month period. Nest and substrate (plant in which nest is built) height increased and vegetative concealment of nests decreased seasonally, but these variables were not related to habitat type. Substrate height varied with substrate species in 1994, and use of individual substrate species varied seasonally. Reproductive phenology differed between the two major habitat types used by gnatcatchers in this study. Whether these seasonal and habitat specific changes in nest placement are adaptive responses to changing environmental conditions that may affect reproductive success has yet to be determined. *Received 15 Feb. 2000, accepted 11 June 2000.*

In open nesting birds, variation in nest placement may affect predation risk (Best and Stauffer 1980, Wilcove 1985, Martin 1988, 1993, Morton et al. 1993; Sockman 1997; but see Filliater et al. 1994) and nest microclimate (Walsberg and King 1978, Walsberg 1981; but see Walsberg 1985). In populations that breed in multiple habitats and over long seasons, nest placement should vary seasonally and by habitat to compensate for seasonally changing and habitat specific environmental conditions that may affect the relationship between nest placement and reproductive success.

The California Gnatcatcher (*Polioptila californica*) is an open nesting, non-migratory passerine that lives in the coastal sage scrub ecosystem of southern California. Its nesting season may last at least 5 months (Sockman 1997), a period over which ambient temperature and precipitation vary considerably (Fig. 1). Its range extends from the Pacific Coast to more than 100 km inland (Atwood 1980) and subsumes several habitat types. Here, I present data on its nest height, height and species of the nest substrate (plant in which the nest is built), and vegetative concealment of nests and how they change with habitat type and phenology of clutch initiation.

METHODS

This study was conducted at Naval Air Station Miramar in San Diego County, California. I have depicted the study site and distribution of breeding pairs previously (Sockman 1997, fig. 1). The site covers approximately 9,600 ha of hilly terrain with several extensive canyons and ridges and extends approximately 20 km from east to west. Elevation ranges from 80–330 m. Dominant habitat types occupied by gnatcatchers are chaparral and coastal sage scrub, which together cover approximately 60% of the site (J. F. O'Leary, unpubl. data).

Data were collected from mid-March to early August in 1994 and 1995, covering the period from the earliest egg-laying to the completion (fledging) of the last known nest each season. Nests were found by searching suitable habitat and by observing birds approach or leave nests. I attempted to find at least one nest of as many pairs as possible throughout the study site and seasons. Nest distribution was fairly uniform across the entire study site and similar between the two years (see Sockman 1997, fig. 1).

I determined the date of clutch initiation in nests found during laying by back calculating using the number of eggs in the nest (laid one per day). I determined date of clutch initiation in nests found during incubation by waiting until eggs hatched and back calculating using a 14 day incubation period (Sockman 1997) and the number of eggs in the nest. I determined date of clutch initiation in nests found with nestlings by estimating the age of nestlings and back calculating as described above. A few nests found during incubation were abandoned before hatching occurred. For these, I could not determine date of clutch initiation, but I used data from these nests when date of clutch initiation was not included in an analysis.

Once laying was completed, I recorded the nest's height (measured from the ground directly below the nest to the bottom of the nest), substrate height (mea-

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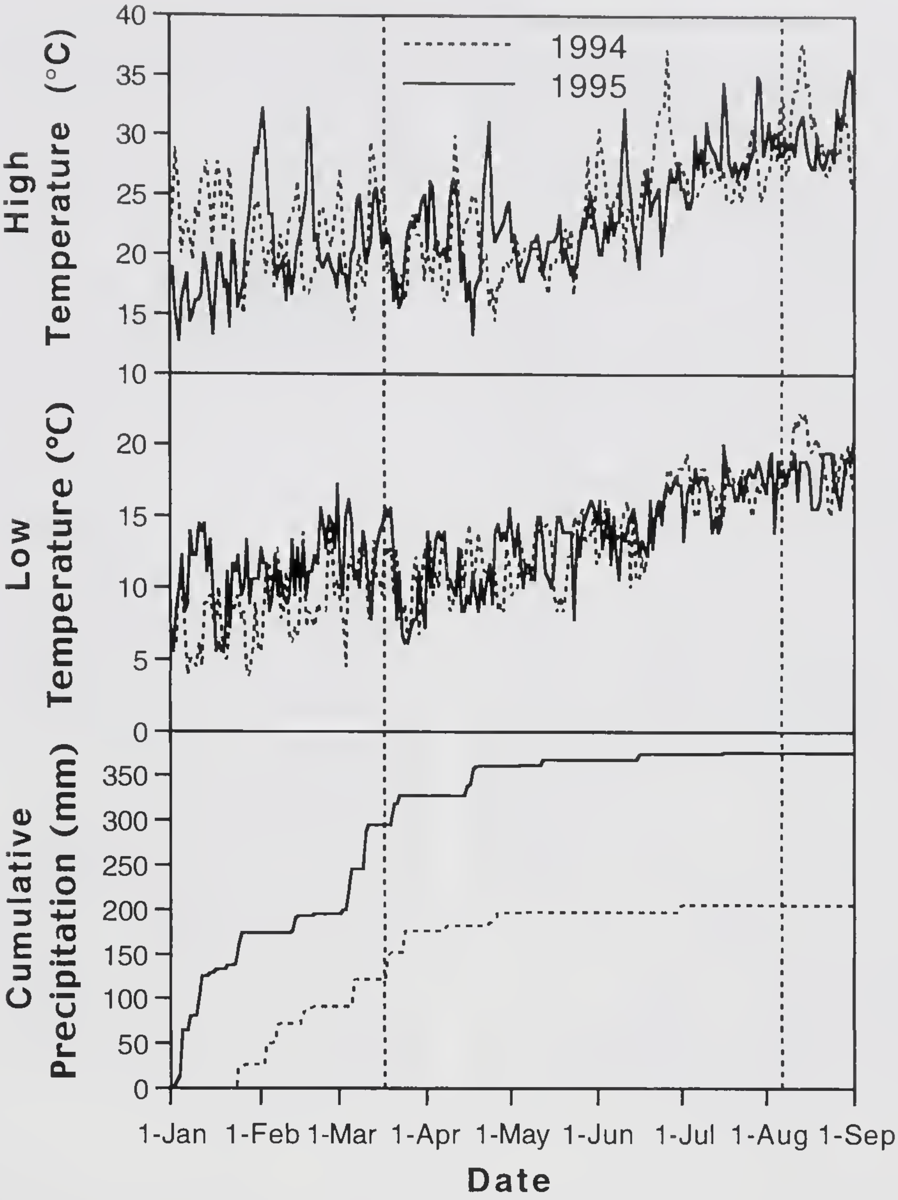

FIG. 1. Daily high and low temperatures and cumulative daily precipitation at Naval Air Station Miramar, San Diego County, California. Vertical, dashed lines delineate the nesting season for California Gnatcatchers.

sured from the ground directly below the nest to the highest point of the shrub within a 30 cm horizontal radius of the nest), lateral vegetative concealment (percent of the nest laterally obscured by vegetation at nest level averaged over estimates from the north, south, east, and west sides 1 m from the nest), and vegetative concealment from above (percent of the nest obscured by vegetation when viewed from 1 m directly above the nest). Because nearly all nests were relatively low and in short substrates, I collected data without the need for a ladder or mirror. Nests were often located on steep slopes and I could view even the few high nests from directly above by standing uphill. I defined relative nest height as the ratio of the nest height to the substrate height and nest ceiling as the difference between substrate height and nest height.

I assigned nests to one of two topographically defined habitat sub-types (arroyo and upland) and recorded the nest substrate species. Both arroyo and upland are sub-types of the coastal sage scrub habitat. I defined arroyos as those areas within the flood plain of ephemeral waterways (i.e., these were the bottoms of canyons). I defined upland as those areas corresponding to the sides of these canyons or to mesas above such canyons. The primary rationale for distinguishing between the two habitat sub-types (hereafter habitats or habitat types) was their profound qualitative difference in plant-species composition. The arroyos were dominated by *Baccharis sarothroides* and the uplands by plant species typical of coastal sage scrub, including *Artemisia californica, Eriogonum fasciculatum, Salvia mellifera, Salvia apiana,* and others. Although each species was sometimes found in either habitat, the two habitats differed markedly in species composition, and I analyzed only nests that I could unambiguously assign to one of the habitats. Temperatures and precipitation were recorded from central locations on the study site (see Sockman 1997).

To maximize the statistical independence among sampling units, I analyzed one nest per breeding pair, randomly selecting one when multiple nests per pair per year were available. Thus, analyses are not necessarily conducted with first nests of a pair. For statistical analyses, I used SuperANOVA 1.11 (Abacus Concepts, Inc., Berkeley, California), Excel 98 (Microsoft Corporation, Redmond, Washington), and StatView 5.0 (SAS Institute, Inc., Cary, North Carolina), each for the Macintosh. I used a contingency table analysis to determine if frequency of substrate species use differed between years. The distributions of each dependent variable used in the parametric statistical analyses described below did not significantly differ from normal (Kolmogorov-Smirnov Tests for Normality of Distribution: $P > 0.05$ for each test). I analyzed each of the two years separately and used two MANCOVA models (for each year) to determine how nest height, substrate height, and vegetative concealment varied seasonally and with respect to habitat type. Nest height, relative nest height, nest ceiling, and substrate height were dependent variables in the first model, and lateral vegetative concealment and vegetative concealment from above were dependent variables in the second. Date of clutch initiation (covariate), habitat type, and their interaction were independent variables for both models. The interaction term was not statistically significant in these models and was therefore removed from the analyses. I used ANOVA to determine whether variation in date of clutch initiation (dependent variable) was explained by habitat type (independent variable).

I used additional analyses to examine the relationships among significantly related variables in the above multivariate analyses. I regressed substrate height, nest height, and lateral vegetative concealment individually on date of clutch initiation. I used an ANOVA model to determine how the date of clutch initiation (dependent variable) varied according to substrate species (independent variable), a MANOVA model to determine how substrate height and nest height (dependent variables) varied according to substrate species (independent variable), and an ANOVA model to determine how lateral vegetative concealment (dependent variable) varied according to substrate species (independent variable). In analyses with substrate species as a variable, I included only those species used as nest substrates at least five times and used Fisher's protected least significant difference for post-hoc analyses. I report both multivariate Wilks' λ P values and P values from univariate tests.

RESULTS

I used 107 nests in analyses, 58 from 1994 and 49 from 1995 [not all nests were used in all analyses (see Methods)]. Breeding pairs were widely distributed across the study area and were generally associated with major canyons. Clutch-initiation dates of randomly selected nests ranged from 18 March–3 July.

In arroyos, gnatcatchers initiated clutches [1994: $\bar{x}$ = 16 Apr ± 6.19 days (SE), $n = 18$; 1995: $\bar{x}$ = 13 Apr ± 6.53 days, $n = 8$) approximately 2 weeks earlier on average than in upland habitat (1994: $\bar{x}$ = 2 May ± 5.17 days, $n = 37$; 1995: $\bar{x}$ = 4 May ± 4.38 days, $n = 40$). The difference was marginally significant in both years (ANOVA: 1994: $F_{1,53} = 3.74$, $P = 0.058$; 1995: $F_{1,46} = 4.38$, $P = 0.042$). Note that these analyses were not conducted exclusively with each pair's first nest but rather with a randomly selected nest from each pair when more than one per pair were available.

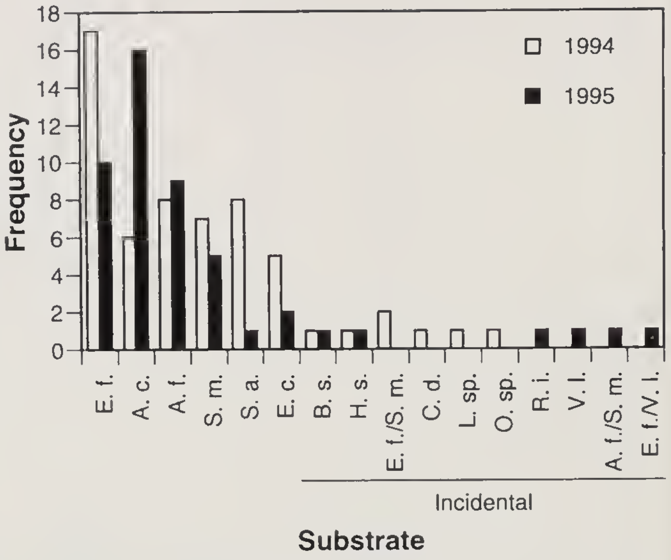

FIG. 2. Frequencies of nest substrates in the California Gnatcatcher. For statistical comparison between 1994 and 1995 frequencies, a substrate with fewer than 5 nesting events for 1994 and 1995 combined was termed "incidental" and excluded. E. f. = *Eriogonum fasciculatum*, A. c. = *Artemisia californica*, A. f. = *Adenostoma fasciculatum*, S. m. = *Salvia mellifera*, S. a. = *Salvia apiana*, E. c. = *Eriodictyon crassifolium*, B. s. = *Baccharis sarothroides*, H. s. = *Haplopappus squarrosus*, E. f./S. m. = *Eriogonum fasciculatum/Salvia mellifera* complex, C. d. = *Cneuridium dumosum*, L. sp. = *Lonicera* sp., O. sp. = *Opuntia* sp., R. i. = *Ribes indecorum*, V. l. = *Viguiera laciniata*, A. f./S. m. = *Adenostoma fasciculatum/Salvia mellifera* complex, E. f./V. l. = *Eriogonum fasciculatum/Viguiera laciniata* complex.

Gnatcatchers nested in a variety of shrub species (Fig. 2), but some species, notably *Eriogonum fasciculatum* and *Artemisia californica*, were used substantially more frequently than others. If incidental (occasionally used) species (shrubs nested in fewer than five times in 1994 and 1995 combined) were excluded, gnatcatchers showed a shift in substrate use from 1994 to 1995 (Contingency Table Test: $\chi^2 = 16.26$, 5 df, $P = 0.006$).

Each year, nest height, substrate height, relative nest height, and nest ceiling combined in a multivariate analysis were related to date of clutch initiation (MANOVA: 1994: Wilks' λ $F_{4,49} = 4.46$, $P = 0.004$; 1995: Wilks' λ $F_{4,42} = 2.67$, $P = 0.045$) but not to habitat type (MANOVA: Wilks' λ $P > 0.05$ for each year). Inspection of the univariate statistics indicated that in each year substrate height (ANOVA: 1994: $F_{1,52} = 13.50$, $P < 0.001$; 1995: $F_{1,45} = 6.51$, $P = 0.014$) and nest height (ANOVA: 1994: $F_{1,52} = 14.74$, $P < 0.001$; 1995: $F_{1,45} = 7.22$, $P = 0.01$) significantly increased with date of clutch initiation (Fig. 3) but relative nest height and nest ceiling did not (ANOVA: $P > 0.05$ for each variable in each year).

Each year, lateral vegetative concealment and vegetation concealment from above combined in a multivariate analysis were related to date of clutch initiation (MANOVA: 1994: Wilks' λ $F_{2,51} = 5.45$, $P = 0.007$; 1995: Wilks' λ $F_{2,44} = 6.38$, $P = 0.004$) but not to habitat type (MANOVA: Wilks' λ $P > 0.05$ for each year). Univariate statistics indicated that lateral vegetative concealment declined (ANOVA: 1994: $F_{1,52} = 6.36$, $P = 0.015$; 1995: $F_{1,45} = 12.32$, $P = 0.001$) and vegetative concealment from above did not change (ANOVA: 1994: $F_{1,52} = 2.15$, $P > 0.05$; 1995: $F_{1,45} = 0.90$, $P > 0.05$) with date of clutch initiation (Fig. 3).

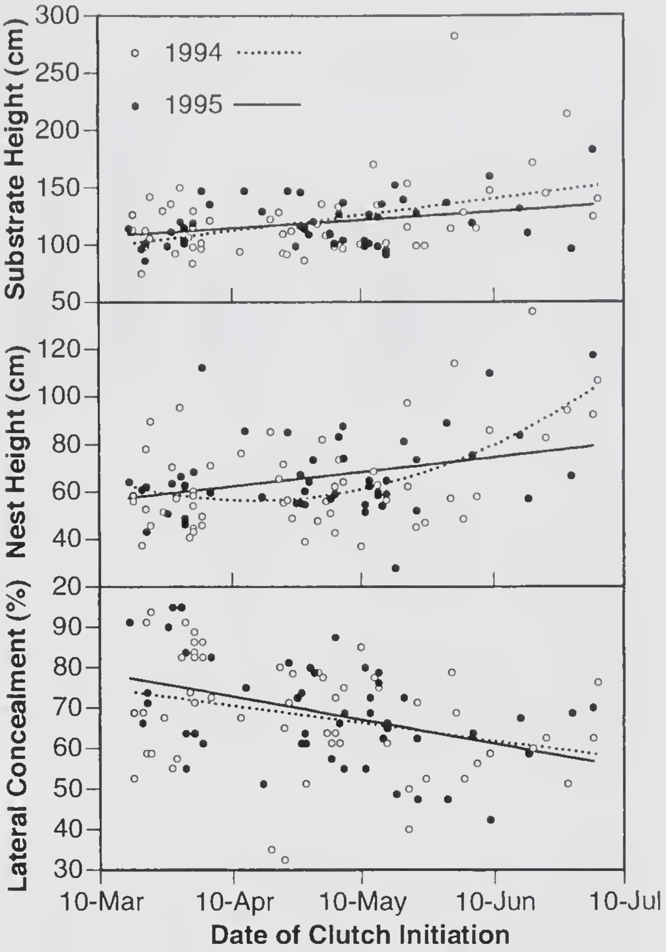

FIG. 3. Change in substrate height, nest height, and lateral vegetative concealment with respect to date of clutch initiation in nests of the California Gnatcatcher.

To further assess the relationships among those variables that showed significant relationships in the above multivariate analyses, I regressed substrate height, nest height, and lateral vegetative concealment individually on date of clutch initiation. Each year, date of clutch initiation explained a small but statistically significant percentage of variation in substrate height (Linear Regression: 1994: $F_{1,53} = 11.82$, $P = 0.001$, $R^2 = 0.18$; 1995: $F_{1,46} = 5.26$, $P = 0.026$, $R^2 = 0.10$), nest height (Linear Regression: 1994: $F_{1,53} = 13.53$, $P < 0.001$, $R^2 = 0.20$; 1995: $F_{1,46} = 5.22$, $P = 0.027$, $R^2 = 0.10$), and lateral vegetative concealment (Linear Regression: 1994: $F_{1,53} = 5.54$, $P = 0.022$, $R^2 = 0.10$; 1995: $F_{1,46} = 9.74$, $P = 0.003$, $R^2 = 0.18$). The curvilinear appearance of nest height plotted against date of clutch initiation (Fig. 3) suggested that some of these regressions may be better described by quadratic than by linear equations. The addition of a date^2 term to the linear regressions above resulted in a significant improvement of the fit of the regression model for 1994 nest height (Multiple Regression: $F_{2,52} = 11.99$, $P < 0.001$, adjusted $R^2 = 0.29$) but not for any of the other regressions (Fig. 3).

If nest placement varied with substrate species and use of substrate species varied seasonally, then seasonally changing nest-placement characteristics might be caused by a seasonal shift in substrate species. To examine this, I analyzed the relationships between substrate species and date of clutch initiation, between substrate species and each of substrate height and nest height, and between substrate species and percent lateral concealment. Each year (ANOVA: 1994: $F_{4,39} = 2.96$, $P = 0.031$; 1995: $F_{3,36} = 3.10$, $P = 0.039$), gnatcatchers built nests in *Adenostoma fasciculatum* significantly later than in other plant species (Fig. 4). In 1994, both substrate height (ANOVA: $F_{5,45} = 10.98$, $P < 0.001$) and nest height

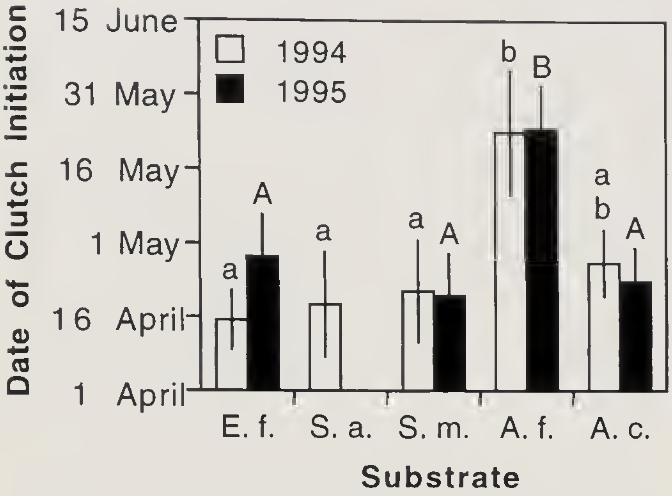

Fig. 4. Change in date of clutch initiation (mean ± 1 SE) with respect to nest substrate species in California Gnatcatchers. Abbreviations are defined and samples sizes shown in Fig. 2. Species used as a substrate fewer than five times (i.e., *Salvia apiana* in 1995) were excluded from this analysis. Within a year, species without a letter in common were significantly different ($P < 0.05$) based on post-hoc analyses.

(ANOVA: $F_{5,45} = 5.10$, $P < 0.001$) were related to substrate species (MANOVA: Wilks' λ $F_{10,88} = 4.81$, $P < 0.001$). These relationships were primarily because *A. fasciculatum* was a taller substrate than other species and because nests built in *A. fasciculatum* were higher than those built in other substrates (Fig. 5). In 1995, the relationship between substrate species and substrate and nest height was not significant (MANOVA: Wilks' λ $P > 0.05$). In neither year was lateral vegetative concealment significantly related to substrate species (ANOVA: 1994: $F_{5,45} = 2.05$, $P > 0.05$; 1995: $F_{3,36} = 1.70$, $P > 0.05$).

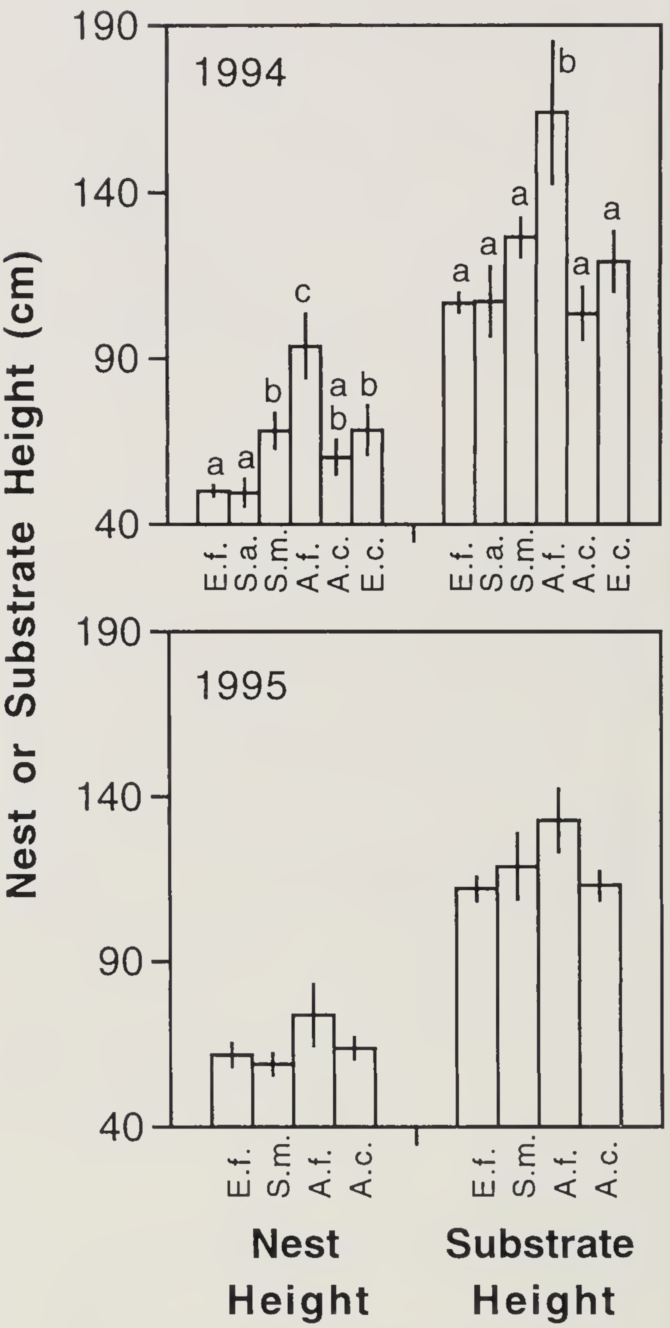

FIG. 5. Change in nest and substrate height (mean ± 1 SE) with respect to substrate species in California Gnatcatchers. Abbreviations are defined and samples sizes shown in Fig. 2. Species used as a substrate fewer than five times (i.e., *Salvia apiana* in 1995) were excluded from this analysis. Species without a letter in common were significantly different ($P < 0.05$) based on post-hoc analyses.

DISCUSSION

Over two approximately 16-week clutch initiation seasons, California Gnatcatchers built nests in a variety of plant species, similar to findings previously published for this species (Grishaver et al. 1998). Nest height, substrate height, and vegetative concealment varied seasonally, but I could not determine whether this reflected a seasonal change in choice or in availability of nest sites. Braden (1999) found that nest placement in California Gnatcatchers is not random with respect to the concealment or species of substrates, suggesting that nest-site selection is not entirely based on availability of sites. Still, I cannot rule out the possibility that seasonal changes in availability of sites gave rise to the seasonal changes in nest placement I observed.

The finding that date of clutch initiation differed between habitats (although only marginally) is similar to previous findings in which gnatcatcher nesting phenology depended on habitat characteristics such as grass and forb cover and increased number of perennials (Braden et al. 1997). I did not quantify habitat-specific differences in vegetative characteristics, but qualitative differences in species composition between the two habitat types were profound and may have given rise to the differing phenologies of clutch initiation. In successive nesting attempts, individual pairs would sometimes move from arroyo to adjacent upland, suggesting that perhaps the differing phenology of nest initiation was not due to a difference between birds nesting in arroyo versus upland.

Adenostom fasciculatum was used as a nest substrate later in the season and, in 1994, was taller than other substrates. This raises the possibility that the 1994 seasonal increase in substrate height was a consequence of a seasonal shift in substrate species. The same logic applies to the seasonal increase in nest height, in that nest height in 1994 was also higher in *A. fasciculatum* than in other substrate species. However, in 1995 substrate height and nest height were not related to substrate species and both substrate height and nest height still increased. This indicates that, at least in some cases, substrate and nest height increase seasonally and independently of seasonal changes in substrate species.

Variation in nest placement affects the probability of nest predation in the California Gnatcatcher (Sockman 1997). Risk of nest predation does not change seasonally and is greatest in the lowest and highest nests and smallest in those nests built in the middle range of nest heights (Sockman 1997). Consequently, minimizing the risk of nest predation alone would not explain the seasonal increase in nest height, but it is possible that seasonal changes in nest height minimize risk of nest predation to the extent that other factors potentially important in nest placement, such as nesting microclimate, are not compromised.

With spring growth, the foliage of coastal sage scrub becomes denser from early spring through summer. If nests were built randomly with respect to concealment, I would predict a seasonal increase in vegetative concealment. I also expected late-season nests to be more concealed than those built early because of the seasonal increase in ambient temperature (Fig. 1) and the fact that, in some species, concealment may affect the nest's microclimate (Walsberg 1985). Previously (Sockman 1997), I found no evidence that variation in vegetative concealment affected nest predation. One possible explanation for the finding that concealment did not increase seasonally is that gnatcatchers seasonally modify nest placement and, in doing so, avoid seasonal increases in nest concealment. It is likely that gnatcatchers position nests in response to factors other than microclimate or risk of nest predation, such as ease of parental access.

Nest site selection in open nesting birds has probably evolved under the collective influence of many factors. In environments where the risk of nest predation is high, optimal nest placement can make the difference between reproductive success and several weeks of wasted time and energy (Best and Stauffer 1980; Wilcove 1985; Martin 1988, 1993; Sockman 1997). Additionally, the inability of eggs and newly hatched altricial nestlings to thermoregulate makes the placement of the nest in an optimal microclimate critical for parents that must balance energetic constraints between time spent on and time spent off the nest (Walsberg 1985). If the tolerance for variation in microclimate is low and risk of nest predation is high, then the fluctuation of climatic and predator regimens expected to occur over a relatively long season should produce commensurate changes in nest placement. The temporal extent of this study (2 5-mo nesting seasons) provided a potentially strong framework for investigating temporal dynamics of nest placement. However, only a small fraction of the variation in nest placement was explained by season, suggesting that other variables may be important.

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EXTENT OF DOUBLE-BROODING AND SEASONAL MOVEMENT OF NESTING FEMALES IN A NORTHERN POPULATION OF WOOD THRUSHES

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ABSTRACT.—Accurate estimates of the amount of double-brooding within a population are an important parameter for assessing the population sustainability of forest birds. In 1998 and 1999, we color-banded adult female Wood Thrushes (*Hylocichla mustelina*) at 70 nests early in the breeding season to assess the frequency of double-brooding in a northern population. We found that double-brooding was a common breeding strategy among Wood Thrushes in southern Ontario. Forty-seven females fledged first broods and 74% ($n = 35$) of them initiated egg-laying in a subsequent nest. It is possible that at least 87% ($n = 41$) of the females were double-brooded, based on the evidence of 6 later nests built within 50 m of successful first nests that were depredated or fledged young before their owners could be identified. Other second-brood nests were probably missed because they were overlooked and because some females moved considerable distances (100–400 m) between nestings. Most birds that failed in their early nesting attempt were not found again on the site, precluding verification of their renesting efforts. *Received 3 April 2000, accepted 4 August 2000.*

Wood Thrushes (*Hylocichla mustelina*) typically raise two broods annually in the southern part of their North American breeding range (Roth et al. 1996) but the number of broods normally produced in northern populations is unclear. It might be supposed that Ontario populations would have second broods less often than populations at more southerly latitudes where nesting may begin as much as a month earlier (Roth et al. 1996). Nevertheless, the literature on other northern populations of Wood Thrushes often refers to the species as double-brooded (i.e., females making a subsequent nesting attempt after fledging a first brood) although documentation is sketchy (Peterjohn and Rice 1991) or relies on information gathered from other, more southerly locales (Pinkowski 1991, Donovan et al. 1995).

In southern Ontario, the extremes of egg dates have been used as a gauge of probable Wood Thrush double-brooding (Peck and James 1998). However, egg dates at similar latitudes in Vermont suggest that double-brooding is infrequent in that region (Kibbe 1985). A problem with using egg dates as an indicator of double-brooding is that they fail to distinguish between actual second brooding attempts and replacement efforts following failure.

A clear understanding of the amount of double-brooding within a population is needed to accurately assess productivity and population viability, an important exercise particularly for Wood Thrushes, which have recently declined over large portions of their breeding range (Sauer et al. 1999). Models of northern Wood Thrush populations have assumed that all females are double-brooded if their first nest succeeds (Donovan et al. 1995, Friesen et al. 1999). However, if the frequency of double-brooding is overestimated, these models overestimate the reproductive output of a population and wrongly conclude that it is a source rather than a sink. The potential importance of double-brooding to estimates of population viability is reflected in the examples of Wood Thrushes and Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) in southern Ontario. Both species have similar rates of nesting success (ca 50%) but because thrushes were considered to be double-brooded and grosbeaks single-brooded, the former but not

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the latter was classified as self-sustaining (Friesen et al. 1999).

We designed a study to validate some of the assumptions used in population modeling of northern Wood Thrushes. Our primary objective was to assess the amount of double-brooding in a population of color-banded birds by tracking individuals and their nests through two breeding seasons. We also investigated the movement of females within the breeding season, whether they remained on site regardless of nesting outcome, and whether all their nests were located in the same general vicinity.

STUDY AREA AND METHODS

Study sites.—Field research was conducted in two regions 50 km apart in southwestern Ontario (43° N, 80° W); Waterloo Region, a fragmented agricultural landscape with 14% forest cover (see Friesen et al. 1999 for a general description of the landscape) and the Niagara Escarpment, an area with 48% forest cover (Ramsay 1996). Wood Thrushes were studied in seven woodlands (sized 2, 4, 8, 10, 18, 24, and 140 ha) in Waterloo Region and three woodlands (sized 20, 20 and 1200 ha) on the Niagara Escarpment. Three sites in Waterloo were clustered together and separated 50–150 m by a highway and a cornfield. The remaining sites in both regions occurred singly and were separated from each other by at least 1 km. Primary habitat at all sites was upland deciduous forest dominated by sugar maple (*Acer saccharum*) with smaller amounts of white ash (*Fraxinus americana*) and American beech (*Fagus grandifolia*).

Data collection.—An intensive nesting and banding study was conducted from mid-May through August in 1998 and 1999 (see Friesen et al. 1999 for a full description of nest searching and monitoring techniques). We attempted to find all nests within each of the woodlands, except the largest forest in each region, using three to six person search teams. In the two large forests, only about a 30 ha section in each could be effectively searched because of time and logistical constraints. Nest searches were conducted at each site at least once a week (on average a minimum of 20 person hours per site per week) throughout the breeding season.

We captured and color banded as many nesting female Wood Thrushes as possible throughout the breeding season using two mist nets positioned in an L-shape within 15 m of active nests. We did not attempt to capture birds in cold or rainy weather and closed the nets for the day if birds were not captured within 1.5 hours. Captured birds were weighed, measured, sexed (Pyle 1997), and fitted with a unique combination of three plastic color bands and one numbered aluminum band. To find second broods, nest searching was intensified around the nests of banded birds that had earlier fledged young. Banded females were classified as double-brooded if they fledged at least one host young from an early nest and initiated egg laying in a subsequent nest.

We modified our capture protocol slightly in the second year of study. In 1998, because of concern over nest disruption, we attempted to capture adult females only after the eggs had hatched. In 1999, we began netting birds as soon as the clutch was complete to improve our chances of confirming double-brooded birds. Our change in capture timing did not seem to negatively impact nesting success; there was no incidence of nest desertion even though many females were captured early in the nesting cycle.

The time interval between first and second broods was defined as the number of days between fledging of the last young from the first nest and the laying of the first egg in the second nest. If second nests were discovered late in the egg stage or in the fledgling stage, the date of the first egg was estimated by back dating 13 days from the first hatching.

Nest trees were marked with flagging tape after the nest outcome was known. At the completion of the nesting season, distances between successful first nests and subsequent nests by the same individual, and distances between nest failures and subsequent renesting sites were measured.

Our study was designed primarily to track double-brooding but not to provide definitive measures on renesting following failure. Researchers from other areas reported that Wood Thrushes with a successful first nest tended to remain in the same area for subsequent nestings that season (Roth and Johnson 1993, Weinberg and Roth 1998). We hoped to trace such individuals throughout the nesting cycle to determine their double-broodedness. We were less confident of following birds that failed on their first attempt because these individuals often abandon a site after nest failure (Weinberg and Roth 1998). Such transients may renest in other woodlots but time and effort considerations dictated that birds disappearing from our study sites could not be monitored for further nesting attempts.

Statistical methods.—A standard χ^2 (Sokol and Rohlf 1981) was used to examine differences in the rates of double-brooding between years. We used a Student's t-test, which assumed unequal variances, to compare the distance between first and second brood nests with the distance between failed nests and the subsequent renesting. Analyses were performed using Microsoft Excel 2000 for Windows.

RESULTS

We banded 70 females at nests where eggs were initiated by 20 June, with 47 of the nests fledging host young. Successful nests were spread fairly evenly between the two study regions, 26 nests in the Waterloo Region and 21 nests on the Escarpment.

Seventy-four percent (n = 35) of females with successful early nests initiated egg-laying

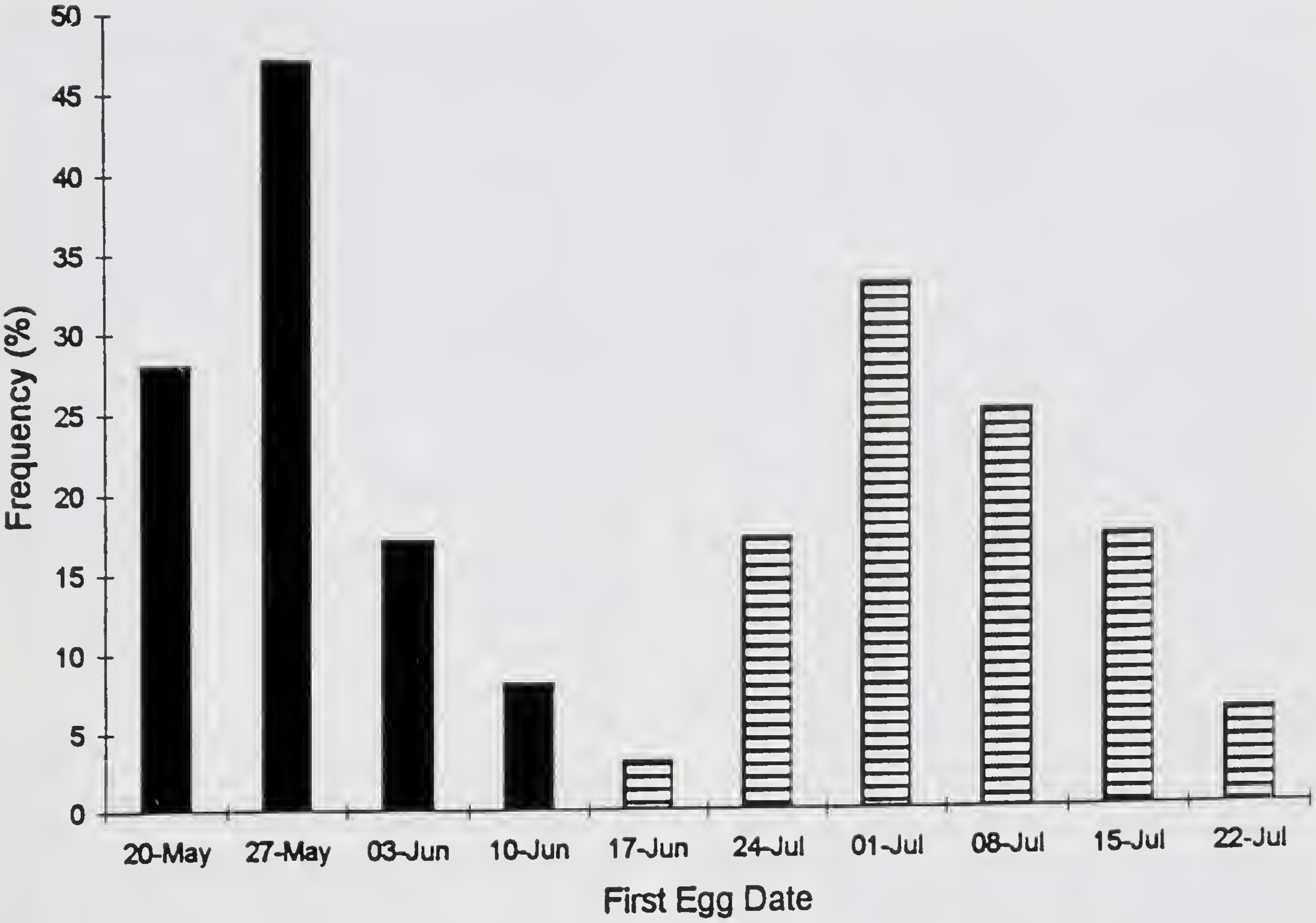

FIG. 1. First egg dates for the first (shaded) and second (striped) nests of double-brooded females.

in a subsequent nest. There was no significant difference ($\chi^2 = 3.08$, 1 df, $P > 0.05$) in the proportion of double-brooding between years: 64% ($n = 16$) in 1998 and 86% ($n = 19$) in 1999. The proportion of double-brooding was similar in each study area; 73% in Waterloo Region versus 76% on the Escarpment. Overall, 36% percent ($n = 25$) of females banded in the early part of the breeding season successfully fledged two broods. There was no evidence of triple-brooding, i.e., two successful broods followed by a subsequent nesting. Two females fledged a first brood and each made two unsuccessful attempts to fledge second broods. We found no evidence of renesting for 13% ($n = 6$) of females following successful early nestings.

The average distance of a second nest from a successful early nest was 72.6 m (±73.6, range 0–400 m with one female reusing her first nest). Half of all second nests (51%, $n = 18$) were built within 50 m of the first nest. Eight females (23%) moved 100–400 m for their second-brood nests. The farthest distance a female dispersed was 400 m to a site across a paved highway. All other double-brooded females remained in the same woodlot for their subsequent nesting attempt.

Average first egg dates in the first successful nests of double-brooded birds was May 24 (±6.4 days, range 13 May to 7 June; Fig. 1); average first egg dates for second-brood nests was 1 July (±7.9 days, range 13 June to 16 July). First eggs of second broods were laid on average 13.4 days (±5.8, range 7–31 days) after the young had fledged from the first nest.

Sixty-five percent ($n = 15$) of unsuccessful females were not encountered after the failure of their early nests. Thirty-five percent ($n = 8$) of unsuccessful females renested on site after failure of their early nests. The average distance of renests from the previous failed nest was 75.8 m (±48.6, range 26–200) which was not significantly different ($t = -0.1805$, 34 df, $P > 0.05$) from the distance between first and second nests.

DISCUSSION

Our results indicate that in southern Ontario, near the northern edge of their breeding range, most Wood Thrushes with successful early nests were double-brooded. The percentage of birds attempting second broods may have been higher than 74% based on the evidence of 6 later nests containing eggs or young found within 50 m of successful early nests. These nests were depredated or fledged young before the adult females could be captured or identified and were built 1–2 weeks after young were fledged from the earlier nests. Further indication that these were probably second nests comes from the fact that all of the active nests (n = 18) that we subsequently found within 50 m of early successful nests belonged to second-brood females from the first nests. If these 6 nests are included as second-broods, the level of double-brooding over the two years of our study was 87%.

It is likely that despite our best searching efforts some nests were missed, especially in the largest forests, and the frequency of double-brooding might be closer to 100%. Confirmation of second nests in our study regions was complicated by the fact that some double-brooded birds moved considerable distances between nestings. Eight females (23%) dispersed more than 100 m after successful first nests. By contrast, the average distance between nestings in a 15 ha fragment in Delaware was 38 m (±49.2; Roth et al. 1996). It may be that some of the six females that were not encountered after successful early nestings dispersed beyond our study areas for subsequent nestings. Radio telemetry techniques are probably the only effective method to adequately verify double-brooding in populations residing in large forests.

At least 35% of banded females that experienced nesting failure remained on site for another nesting effort. Our renesting data are conservative estimates, however, because we might have missed predated first nests of double-brooded females. It is also possible that we overlooked some later renesting efforts or missed renestings that occurred outside our study areas in the large forests. Unsuccessful pairs that remained on our sites traveled about the same average distance between nesting attempts as successful pairs. However, most birds whose nests failed apparently left the study area, a pattern that has been reported for Wood Thrushes elsewhere (Roth and Johnson 1993, Weinberg and Roth 1998).

We did not encounter any instance of early season nesting failure followed by subsequent double-brooding. This observation must be treated cautiously, however, because we might have missed a predated first nest of a double-brooded female; our egg-dates (Fig. 1) indicate that it certainly is possible for a first nesting attempt to fail before 20 May and for a subsequent double-brooding effort to commence before the end of the month. Wood Thrushes farther south than Ontario have additional time during the breeding season to produce two broods following initial failure (Roth et al. 1996). The shorter breeding season may account for the lower overall proportion (36%) of females on our study sites that fledged two broods of young in a year compared to the 51% recorded in Delaware (Roth et al. 1996).

First egg dates of first and second broods suggest two nesting peaks for southern Ontario Wood Thrushes around 24 June and 1 July; the peaks are about a week later than those reported for double-brooded birds from Delaware (Roth et al. 1996). The average time interval of 2 weeks between first and second broods in Ontario is similar to what has been reported for southerly populations (Brackbill 1943, Longcore and Jones 1969, Roth et al. 1996).

Additional studies are needed to determine whether the frequency of double-brooding in southern Ontario is true for other northerly populations of Wood Thrushes. Further investigation is needed to determine whether within-season dispersal commonly occurs amongst females and, if so, the reasons for such movement. More information is also needed on the frequency of renesting following early-season failure and on the movement of birds that have experienced failure.

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NESTING SUCCESS OF YELLOW-BREASTED CHATS: EFFECTS OF NEST SITE AND TERRITORY VEGETATION STRUCTURE

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ABSTRACT.—The effects of habitat and vegetation characteristics on the reproductive success of Yellow-breasted Chats (*Icteria virens*) were examined in central Kentucky. During the 1998 breeding season, 49 nests were located and monitored and the characteristics of nest sites and territories determined. Habitats where nests were located were categorized as old field, linear, or clump, and nests were classified as early or late. Chat nests were located in areas with more foliage and lateral cover than unused sites. However, most nests (55%) were not successful, and variables that differed between nest sites and random locations did not appear to influence nesting success. A diverse and, in an evolutionary sense, novel community of predators may eliminate predictably safe nest sites for chats on our study area. Chats in territories with more foliage cover and less canopy cover were more likely to fledge young. Dense foliage may lower the chances of nest predation by increasing the number of potential nest sites in a territory and may also provide better foraging habitat. *Received 29 Feb. 2000, accepted 18 July 2000.*

When choosing a nest site, songbirds may select habitat patches (Martin and Roper 1988) that improve their chances of successfully fledging young. For example, large shrub patches may contain more potential nest sites for a visually searching predator to investigate (Martin and Roper 1988) and more effectively screen nests and the actions of parents than smaller patches (Holway 1991). Habitat features within patches may also influence nesting success. For example, successful Hermit Thrush (*Catharus guttatus*) nests were characterized by a greater density of white fir (*Abies concolor*) saplings and greater concealment than unsuccessful nests (Martin and Roper 1988), and successful Hooded Warbler (*Wilsonia citrina*) nests had more fern (primarily *Woodwardia areolata* and *Polystichum acrostichoides*) cover than unsuccessful nests (Kilgo et al. 1996). In contrast to these results, other investigators have failed to detect any relationship between the characteristics of either nest patches or nest sites and nesting success (Filliater et al. 1994, Howlett and Stutchbury 1996, Braden 1999). Clearly, additional data are needed concerning the possible relationship between nest-site selection and nesting success.

Habitat features within breeding territories independent of nest sites may also affect reproductive success. For example, nesting success among Northern Cardinals (*Cardinalis cardinalis*) in Texas was positively correlated with the presence of patchy understory foliage and arthropod biomass (Conner et al. 1986). Similarly, California Gnatcatchers (*Polioptila californica*) nested earlier and produced more fledglings when territories included more grass and forb cover, perennial structure, and horizontal perennial homogeneity, with less vertical perennial homogeneity and perennial diversity (Braden et al. 1997).

Yellow-breasted Chats (*Icteria virens*) breed in early successional habitats with an abundance of weedy cover and scattered trees (Palmer-Ball 1996). Dense thickets of blackberry (*Rubus* sp.), multiflora rose (*Rosa multiflora*), and Japanese honeysuckle (*Lonicera japonica*) are commonly used for nesting (Dennis 1958, Thompson and Nolan 1973). Although chats typically nest in areas with dense thickets, little is known about the specific vegetational features at nest sites and within territories that might influence their reproductive success. Burhans and Thompson (1999) reported that chats experienced less predation and higher rates of parasitism in large (>5.5 m diameter) nest patches; however, few specific nest site characteristics were measured. The objective of our study was to examine nest site selection by Yellow-breasted Chats in central Kentucky at the territory, patch, and nest site levels and, specifically, to quantify the vegetation structure at chat nest sites and within territories and to determine which, if any, habitat features were correlated with reproductive success.

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METHODS AND MATERIALS

We studied chats from April–July 1998 at the Central Kentucky Wildlife Management Area, 17 km southeast of Richmond, Madison County, Kentucky. The area (621 ha) consists of a mosaic of deciduous woodlots, old fields, and fencerows. Old fields were dominated by various herbaceous species plus thickets of smooth sumac (*Rhus glabra*) and blackberry (*Rubus allegheniensis*); fencerows included eastern redcedars (*Juniperus virginiana*) and black locusts (*Robinia pseudoacacia*) plus thickets of multiflora rose (*Rosa multiflora*), Japanese honeysuckle (*Lonicera japonica*), smooth sumac, and blackberry.

Beginning in late April, we captured chats in mist nets and banded them with a numbered USFWS leg band and a unique combination of colored plastic bands. We delineated territorial boundaries by monitoring the movements of males and noting the location of singing males and aggressive encounters.

Chat nests were located by following females carrying nest material and searching areas where we observed chats. Once located, nests were checked every three to four days until young fledged or the nest was lost to predation. Nests (and territories) from which at least one young fledged were classified as successful, while those from which no young fledged were classified as unsuccessful. To evaluate the potential influence of time on nesting success, nests were also classified, based on the date of initiation, as either early (before 15 June) or late (after 15 June). We evaluated chat reproductive success using both simple nesting success (number of successful nests/total nests) and the Mayfield method (Mayfield 1975). Survival probabilities between early and late nests and among patch categories (below) were compared using CONTRAST (Sauer and Williams 1989, Hines and Sauer 1989).

Nest sites were assigned to one of three habitat or patch categories: old field, linear, or clump. Old fields were larger than 1 ha and included various grasses and forbs plus scattered small trees and shrubs. Linear habitats were narrow strips (<10 m wide and >0.5 ha) along fencerows, roadsides, and the edges of woodlots. Clumps were defined as areas smaller than 0.5 ha consisting of small trees and shrubs (<10 m tall) and surrounded by old field habitat.

Vegetation structure at chat nests and within territories was quantified using 0.04 ha circular plots (James and Shugart 1970). Nest sites were sampled 2–30 days after either fledging or nest failure to minimize disturbance. Nest site plots were centered at chat nests. To sample vegetation within territories, the approximate center of each territory was located and three circular plots were then located at random distances from the center at compass bearings of 90°, 210°, and 330° (Conner et al. 1986). Data from these plots were averaged. Variables measured in each plot included percent foliage cover at vertical intervals of below 1 m, 1–2 m, and 2–3 m, number of trees less than and greater than 8 cm diameter at breast height (dbh), percent canopy cover, percent ground cover, foliage height, percent lateral cover at vertical intervals of less than 1 m, 1–2 m, and 2–3 m, and percent cover of dominant understory plants such as grasses, forbs, shrubs, and bare ground (see Larison et al. 1998 for methods of estimation). In addition, nest height, substrate, and concealment were measured in nest-site plots. Percent concealment was calculated by estimating how much of a nest was obscured by foliage when viewed at nest height level from 1 m. Each nest was viewed from the four cardinal directions and an average percent concealment determined.

We used stepwise logistic regression to determine which habitat variables best distinguished successful from unsuccessful nests and territories. Successful and unsuccessful nests and territories were first compared using univariate Wilcoxon 2-sample tests (Nadeau et al. 1995, Rabe et al. 1998). Variables with $P < 0.15$ were included in the initial regression model (Nadeau et al. 1995). Subsequently, variables were included (score χ^2 statistic) or removed (Wald's χ^2 statistic) from logistic regression models using a criterion of $P < 0.25$. Kendall correlation coefficients were calculated to ensure that variables were not highly correlated ($\tau_b > 0.40$; Nadeau et al. 1995). Wald's χ^2 statistics were used to assess the contribution of individual variables to the model. Overall model significance was based on log-likelihood χ^2 statistics, classification accuracy (based on a logistic cutpoint of 0.5 to classify nests/territories as successful or unsuccessful), and the Hosmer-Lemeshow lack-of-fit test (Rabe et al. 1998). Positive parameter coefficients in the logistic regression equations indicated that an increase in the value of a variable increased the probability of a nest-site/territory being successful. Conversely, a negative coefficient indicated that as the value of the variable increased, the probability of the nest site/territory being successful decreased.

We also compared nest site and territory vegetation for 19 territories. When a pair made more than one nesting attempt, data were pooled. Values were compared using Wilcoxon 2-sample tests. A stepwise logistic regression model comparing nest site and territory vegetation data was then built using procedures described previously.

Using univariate Wilcoxon 2-sample tests, we also compared the characteristics of early and late nests. Nesting attempts that spanned early and late nesting periods ($n = 10$) and early nests not sampled until the late period ($n = 7$) were deleted to permit better comparison of vegetation around early and late nests. Characteristics of successful and unsuccessful nests for both early and late nests (i.e., successful vs unsuccessful early nests and successful vs unsuccessful late nests) were compared using Wilcoxon 2-sample tests. All analyses were performed using SAS software (ver. 6.09 for VAX Alphaserver; SAS Institute 1989). All values are reported as mean ± one standard error.

RESULTS

Chat nests ($n = 57$) were located in 13 plant species, with blackberry the most frequently

TABLE 1. Results of stepwise logistic regression analysis comparing Yellow-breasted Chat nest-site and territory vegetation characteristics.

Variable	Coefficient	SE[a]	Wald χ^2	*P*
Intercept	−21.514	9.214	5.452	0.019
% foliage cover < 1 m	0.232	0.102	5.189	0.023
% foliage cover 1–2 m	0.120	0.086	1.938	>0.05

[a] Standard error.

used substrate ($n = 26$). Among the other species used by nesting chats were multiflora rose ($n = 7$), Japanese honeysuckle ($n = 5$), roughleaf dogwood (*Cornus drummondi*; $n = 4$), coralberry (*Symphoricarpos orbiculatus*; $n = 3$), black locust ($n = 3$), and eastern redcedar ($n = 3$). Mean nest height was 78.7 ± 4.1 cm, while mean concealment was 73.6 ± 3.1%. Nests abandoned ($n = 3$), destroyed by storms ($n = 4$), or with incomplete data ($n = 1$) were not used for subsequent analyses. Of the remaining 49 nests, 22 (45%) were successful. The daily survival rate (Mayfield 1975) was 0.96 ± 0.007, and rates did not vary among patch types ($\chi^2 = 0.35$, 2 df, $P > 0.05$). Most nests lost to predation were found empty and undisturbed. No chat nest was parasitized by Brown-headed Cowbirds (*Molothrus ater*).

Foliage cover below 2 m was greater at nest sites than in other areas of chat territories and nest sites had more lateral cover below 1 m (Wilcoxon tests: $P < 0.01$). The final logistic regression model predicting the probability that a site would be used as a nest site by chats included two variables: foliage cover below 1 m and from 1–2 m (Log likelihood $\chi^2 = 38.4$, $P < 0.001$; Table 1). The model correctly classified 88.9% of the data used to build the model and provided good fit to the data (Hosmer-Lemeshow lack-of-fit; $\chi^2 = 1.03$, 7 df, $P = 0.99$).

Univariate Wilcoxon 2-sample tests revealed significant ($P < 0.05$) differences between successful and unsuccessful nests for two of 17 variables. Successful nests had higher forb cover and lower shrub cover than unsuccessful nests (Table 2). Three other variables (nest height, percent foliage cover at 2–3 m, and number of trees > 8 cm dbh) met our criterion of $P < 0.15$ (Table 2) and were used in the stepwise logistic regression model-building procedure. Only one nest-site char-

TABLE 2. Results of univariate comparisons (Wilcoxon 2-sample tests) between successful and unsuccessful chat nests.

	Successful ($n = 22$)		Unsuccessful ($n = 27$)		
Variable	Mean	SE	Mean	SE	*P*
Nest height (cm)	82.9	4.9	75.2	6.4	0.07
% nest concealment	75.4	4.5	72.0	4.4	>0.05
# trees < 8 cm dbh	61.8	17.0	53.9	6.4	>0.05
# trees > 8 cm dbh	4.3	1.3	7.8	1.7	>0.05
Foliage height (m)	2.2	0.3	2.4	0.3	>0.05
% foliage cover < 1 m	90.5	2.2	89.9	1.7	>0.05
% foliage cover 1–2 m	37.0	3.6	39.9	3.4	>0.05
% foliage cover 2–3 m	7.7	2.4	13.1	2.9	0.10
% lateral cover < 1 m	99.1	0.3	95.4	2.1	>0.05
% lateral cover 1–2 m	63.6	5.5	59.2	5.0	>0.05
% lateral cover 2–3 m	38.6	6.5	43.1	5.1	>0.05
% canopy cover	18.2	4.6	28.6	4.8	>0.05
% ground cover	97.5	1.7	97.0	1.4	>0.05
% grass cover	11.4	3.1	17.8	4.2	>0.05
% forb cover	57.5	7.8	31.1	6.8	0.01
% shrub cover	30.1	6.5	51.2	7.0	0.04
% bare ground	0.1	0.1	0.2	0.2	>0.05

TABLE 3. Results of stepwise logistic regression analyses comparing vegetation characteristics of successful and unsuccessful Yellow-breasted Chat nests and territories.

Variable	Coefficient	SE	Wald χ^2	P
Nest model:				
Intercept	−0.986	0.492	4.019	0.045
% forb cover	0.019	0.008	5.174	0.023
Territory model:				
Intercept	−6.027	4.985	1.461	>0.05
% foliage cover < 1 m	0.154	0.093	2.736	>0.05
% canopy cover	−0.074	0.059	1.589	>0.05

acteristic, percent forb cover ($P < 0.25$), was included in the final logistic regression model comparing successful and failed nests (Log likelihood $\chi^2 = 5.61$, $P = 0.018$; Table 3). The model correctly classified 66% of the data used to build the model (Hosmer-Lemeshow lack-of-fit test; $\chi^2 = 5.74$, 6 df, $P = 0.45$).

We sampled vegetation in 14 successful and 5 unsuccessful chat territories. Successful territories had greater ($z = 2.24$, $P = 0.02$) foliage cover below 1 m than unsuccessful territories. Four other variables (foliage height, percent foliage cover at 2–3 m, canopy cover, and percent bare ground) met our criterion of $P < 0.15$ and were used in the initial logistic regression model. The final model predicting the probability that young would fledge in a chat territory included two variables, percent foliage cover below 1 m and canopy cover (Log likelihood $\chi^2 = 8.35$, $P = 0.015$; Table 3). The canopy cover coefficient was negative, with successful territories having less canopy cover ($\bar{x} = 16.0 \pm 4.1\%$) than unsuccessful ($\bar{x} = 31.6 \pm 5.4\%$) territories. The model correctly classified 67% of the data used to build the model (Hosmer-Lemeshow lack-of-fit test; $\chi^2 = 5.15$, 7 df, $P = 0.64$).

The daily survival rates of early (0.96 ± 0.009) and late (0.97 ± 0.011) nests did not differ ($\chi^2 = 0.47$, 1 df, $P > 0.05$). However, differences between early (1.1 ± 0.3) and late (1.8 ± 0.4) nests in the mean number of fledglings approached significance ($z = 1.91$, $P = 0.06$). Several habitat variables of early and late nests differed (Fig. 1). Early nests had less lateral cover below 1 m but greater foliage cover and lateral cover between 2–3 m than late nests (Fig. 1). Small (<8 cm dbh) trees were more numerous around early nests ($z = 2.82$, $P = 0.005$) and foliage height ($z = 1.99$,

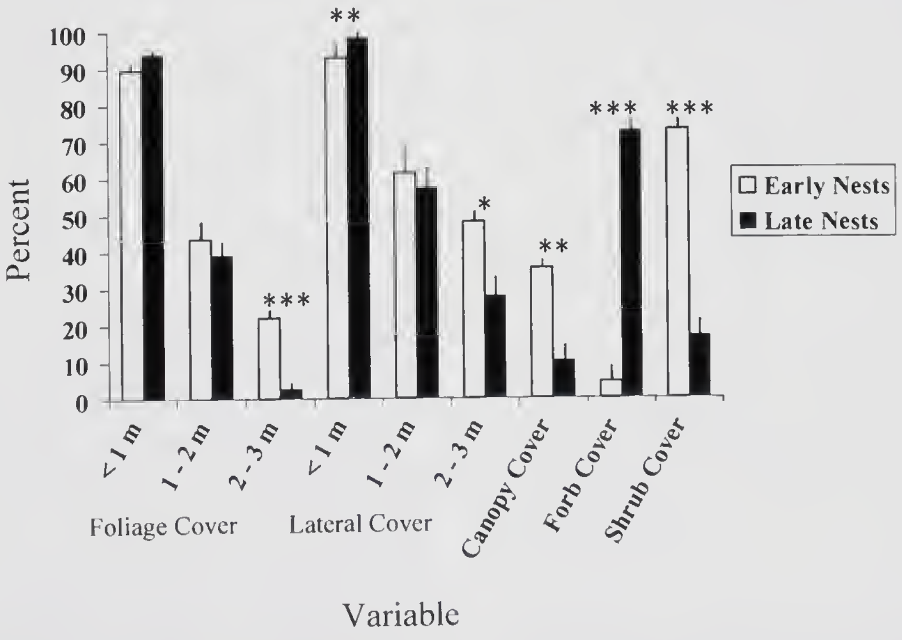

FIG. 1. Comparison of the characteristics of early (before 15 June) and late (after 15 June) Yellow-breasted Chat nests (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

$P = 0.046$), canopy cover, and shrub cover were also greater at early nests. Late nests had more forb cover than early nests (Fig. 1).

DISCUSSION

Nearly half of the Yellow-breasted Chat nests in our study were located in blackberry, as were many chat nests in Missouri (Burhans and Thompson 1999). Blackberry commonly grows in dense thickets that, in addition to providing concealment, could potentially provide additional protection from predators via the presence of numerous thorns. However, Ricketts (1999) found no differences in the daily survival rates of chat nests located in blackberry versus other plant species. While dense, thorny thickets of blackberry could potentially impede some predators (e.g., large mammalian predators such as raccoons, *Procyon lotor*), other predators, including snakes and small mammals are likely not deterred by such vegetation.

The nests of Yellow-breasted Chats in our study were located in areas with more foliage (and lateral) cover than unused sites. Despite such placement, most chat nests were not successful; we found no differences between successful and unsuccessful chat nests in foliage and lateral cover or percent concealment. Similarly, Braden (1999) found that nest placement by California Gnatcatchers was not random, with nests placed in locations with more cover and taller vegetation than random locations. However, variables that differed between nest sites and random locations did not influence nesting success. Other investigators have reported similar results (Conner et al. 1986, Holway 1991, Howlett and Stutchbury 1996, Wilson and Cooper 1998).

One possible explanation for the absence of differences in the characteristics of successful and unsuccessful nests in chats and other species is the presence of a diverse community of predators. Among the many potential nest predators on our study site in central Kentucky were coyotes (*Canis latrans*), raccoons, feral cats (*Felis domesticus*), eastern chipmunks (*Tamias striatus*), long-tailed weasels (*Mustela frenata*), Blue Jays (*Cyanocitta cristata*), American Crows (*Corvus brachyrhynchos*), black rat snakes (*Elaphe obsoleta*), and blue racers (*Coluber constrictor*). Filliater and coworkers (1994) found no relationships between the characteristics of nest sites and nesting success in a population of Northern Cardinals and suggested that environments with a variety of predators, each using a different search strategy, may eliminate predictably safe nest sites. Passerines in environments where nest predation is unpredictable (Schmidt and Whelan 1999) and where most or all nest locations are subject to similar predation risk may respond by following simple behavioral rules for nest placement (Filliater et al. 1994). For chats, these rules would include placing nests low (≤1 m above the ground), in locations with little or no canopy cover, and dense foliage cover that provides some concealment. These rules may be of only limited benefit in predator-rich communities (Filliater et al. 1994), but even limited benefits may be of value (Schmidt and Whelan 1999).

Another possible explanation for our results is that there has been strong selection on nest site choice by Yellow-breasted Chats in the eastern United States. However, this selection occurred in an environment that no longer exists in most areas. Chats occupy early successional habitats and, throughout much of eastern North America prior to the arrival of Europeans, such habitats were less abundant and may have been limited to natural forest openings caused by windstorms or fire (Palmer-Ball 1996). Man-made openings created by forest management practices (e.g., clearcutting) are readily used by chats (Thompson et al. 1992). In natural openings surrounded by extensive tracts of deciduous forest, the predator community differed, and, where larger tracts of forest remain, still differs (Suarez et al. 1997) from that found in many areas now occupied by chats in the eastern United States, including our study site. Some predators present on our study site were not present in the past; others were absent or uncommon (Wilcove 1988; Durner and Gates 1993). It is likely, therefore, that a primary breeding habitat used by chats in the past (natural forest openings) supported a less diverse predator community. If so, chats on our study area might be selecting nest sites based on behavioral rules developed in response to a predator community that no longer exists.

Although variables that differed between chat nest sites and random locations (foliage cover below 2 m) did not influence nesting success in our study, successful nests had more forb cover than unsuccessful nests. In addition, at the territory scale, chats in our study were more likely to fledge young in territories with more foliage cover below 1 m (including forb cover) and less canopy cover. Chats glean insects from low foliage in dense thickets and occasionally forage on the ground (Dunn and Garrett 1997). Thus, one explanation for our results is that increased foliage cover might provide better foraging substrate and more arthropods for chats. Similarly, Conner and coworkers (1986) reported that Northern Cardinals had greater fledging success in territories with more understory foliage (and arthropod biomass). Greater forb and foliage cover may also increase the number of potential nest sites in a territory, and increase the number of potential sites for predators to examine, lowering the chance of nest predation (Martin and Roper 1988).

Although we found no differences in daily survival rates between early and late nests, the mean number of young fledged per nest increased later in the breeding season. Other investigators have also reported increased nesting success later in the breeding season (Longcore and Jones 1969, Thompson and Nolan 1973, Best 1978, Filliater et al. 1994). One possible explanation for such seasonal differences in early successional habitats is reduced predation pressure later in the season, particularly by snakes. Roseberry and Klimstra (1970:264) noted that snakes were frequently observed in May but became "progressively more scarce in June and July" in southern Illinois. Similarly, Nolan (1978) attributed a July rise in the reproductive success of Prairie Warblers (*Dendroica discolor*) and other birds in a study area in Indiana to decreased snake activity.

Daily survival rates did not vary among habitat or patch types in our study. Burhans and Thompson (1999) found that chats nesting in larger patches experienced less predation; however, they defined large and small patches as being either more or less than 5.5 m diameter, respectively (the smallest patch was 0.3 m diameter). Thus, we may not have noted differences among patch types because most or all of our patches were large, based on Burhans and Thompson's (1999) definition. Patch size and shape may influence nest predation rates via differences in the number of potential nest sites (Martin and Roper 1988) and the screening of nests and parental activity (Holway 1991); detecting such differences may require examination of smaller patches than those observed in our study.

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THE EFFECTS OF FARM FIELD BORDERS ON OVERWINTERING SPARROW DENSITIES

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ABSTRACT.—Wintering birds that use farm fields may benefit from strips of uncultivated, grassy, and weedy vegetation, called field borders. Field borders were established on 4 farms in the North Carolina coastal plain in Wilson and Hyde counties in the spring of 1996. In February of 1997 and 1998, bird numbers on field edges and field interiors, with and without field borders, were surveyed using strip transect and line transect methods. Most (93%) birds detected in field edges were sparrows, including Song (*Melospiza melodia*), Swamp (*Melospiza georgiana*), Field (*Spizella pusilla*), Chipping (*Spizella passerina*), White-throated (*Zonotrichia albicollis*), and Savannah (*Passerculus sandwichensis*) sparrows and Dark-eyed Juncos (*Junco hyemalis*). We detected more sparrows on farms with field borders than on farms with mowed edges. This difference was most pronounced in field edges where field borders contained 34.5 sparrows/ha and mowed edges contained 12.9 sparrows/ha. Sparrow abundance did not differ by treatment in field interiors. Sparrow density in field borders was intermediate to wintering sparrow densities reported in other studies. These results suggest that establishing field border systems may be an effective way to increase densities of overwintering sparrows on farms in the southeastern U.S. coastal plain. *Received 8 March 1999, accepted 20 June 2000.*

Management of grain farms has changed dramatically in the past century. Economic pressures and advances in farm equipment have led farmers to make fields and farmed openings larger (Warner 1994), thereby reducing edge habitats. Advances in machinery, herbicides, and transgenic crops have enabled farmers to effectively control most non-crop vegetation in and around fields. These trends in agriculture have led to a dramatic alteration of the quantity and quality of wildlife habitat on farms and may have contributed to population declines of many farmland birds, including several species of sparrows (Warner 1994, LeGrand 1996).

The value of field edge habitat for farmland wildlife in general and emberizids in particular has been investigated in Britain and the Midwestern United States (O'Conner and Shrubb 1986, Best et al. 1995), but has not been extensively studied in the southeastern U.S. Many farmland sparrows, including Song (*Melospiza melodia*), Field (*Spizella pusilla*), and Savannah (*Passerculus sandwichensis*) sparrows rely on an interspersion of habitats in various seral stages (Bent 1968, Wheelwright and Rising 1993, Carey et al. 1994). Early successional habitats may be the most limiting habitat type on modern farms.

Sparrow populations may benefit from field borders, strips of uncultivated, grassy, and weedy vegetation along the edges of fields. The early successional habitat of field borders provides important breeding season nesting cover (Puckett et al. 1995, Marcus 1998) and also may be critical for overwintering sparrows by providing habitat for foraging, avoiding predators, and gaining protection from the elements. Food and cover have been implicated as resources potentially limiting winter densities of sparrows (Pulliam and Enders 1971, Davis 1973, Lima 1990, Watts 1990). Field borders potentially provide these resources and may increase usable habitat space on farmland for overwintering sparrows. The cost of managing to increase the amount of field border habitat may be minimal because net profits on field edges are less than in field interiors (Morris 1998) and several United States Department of Agriculture natural resource programs provide funds to subsidize farmers who leave field borders untilled. The objective of this study was to test the hypothesis that the presence of field borders increases the density of sparrows using farm fields, both in the edge and interior of fields.

STUDY SITES AND METHODS

Study sites.—Field work was conducted on two study sites in the North Carolina coastal plain, one in Wilson County and one in Hyde County. Each study

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site was divided into four farms. At each site field borders were established around each field on two farms, and two farms were left without field borders as controls. Throughout this paper "field borders" refer to the habitat enhancement strips in experimental fields, "mowed edges" refer to the corresponding area of mowed vegetation and crop residue on control fields, and "field edge" refers to the margin of a field with or without a field border. The farms contained similar crops (except where noted) and amount of woody edge and were located at least 1.7 km apart. Farms within each site were selected to be as similar as possible; however, some differences in management and surrounding landscapes existed.

The four Wilson County farms (77° 53′ W, 35° 42′ N), located in the upper coastal plain, averaged 250 ha ± 18 ha (SE) and contained irregularly shaped row-crop fields less than 2.5 ha each. Each farm contained 20–22 fields which comprised 43 ± 3% of each farm and were intermixed with a mosaic of house sites and timber stands of various ages. Field borders 5–10 m wide were established at field edges adjacent to drainage ditches, roadsides, and woodlines. Fields contained residue of corn (*Zea mays*), soybeans (*Glycine* sp.), and tobacco (*Nicotiana tabacum*).

The four farms in Hyde County (76° 05′ W, 35° 25′ N), located in the lower coastal plain, averaged 167 ± 18 ha and consisted of six to ten rectangular fields of 8–12 ha. The fields, arrayed in contiguous openings of over 200 ha, were separated only by drainage ditches or dirt roads. Farmed openings were bordered on one or two sides by a timber stand, and row-crop fields comprised 68 ± 1% of each farm. These farms were located on drained wetlands with organic soils and were typical of large ditch to ditch commercial agriculture of the lower coastal plain. Field borders 5–10 m wide were established along ditches located between fields. Fields contained residues of corn and soybeans. Field border farms were planted to winter wheat 5 cm tall at the time of the surveys in 1998.

Field borders were established at both sites in the spring 1996 by allowing vegetation to colonize the field edges. Field borders comprised 13.4% of tilled land in Wilson County and 9.8% of tilled land in Hyde County. Edges of control fields consisted of narrow (< 2 m) strips of annual vegetation that were mowed in early winter of each year.

Field borders in Wilson County consisted primarily of dead stalks of dog fennel (*Eupatorium capillifolium*), broomsedge (*Andropogon virginicus*), dormant blackberry (*Rubus argutus*), giant cane (*Arundinaria giganteum*), sapling sweetgum (*Liquidambar styraciflua*), and red maple (*Acer rubrum*). Field borders in Hyde County consisted primarily of dead stalks of dog fennel and fall panicum (*Panicum* sp.), dormant blackberry and giant cane, and sapling wax myrtle (*Myrica cerifera*).

Vegetation.—Vegetative structure of field edges was measured in February of 1997 and 1998 by visually estimating the percent cover and median height of standing vegetation. The percent cover was defined as the percentage of the 10 m strip that contained standing vegetation over 15 cm.

A detailed analysis of the composition and structure of vegetation in field edges was conducted in the summer 1997. Vegetative structure was measured using a modified vegetation profile board (Nudds 1977). A 2 m × 8 cm pole was placed upright in the vegetation and the observer stood 2.5 m away on a line perpendicular to the field's edge. The observer estimated the percentage of the pole obscured at 0–0.25 m, 0.25–0.5 m, 0.5–1.0 m, 1.0–1.5 m, and 1.5–2 m. An index of vertical structure was derived by averaging these 5 values.

Vegetative composition was measured using a modified Daubenmire grid (Daubenmire 1959). A 0.5 × 0.5 m grid was held 1 m above the ground and the absolute cover of vegetation within the grid was visually estimated. Percent cover of bare ground, leaf litter, grasses (including rushes and sedges), forbs (all broad-leafed, non-woody vegetation), and woody vegetation were estimated. Each category was measured independently; thus, the totals could sum to more than 100% when vegetation was multi-layered.

Bird surveys.—Bird densities were measured using line transect and strip transect methods (Lancia et al. 1994). Because the probabilities of detecting a bird on an open field and in the brushy cover of field edges were unequal, field interiors and field edges were surveyed separately.

Fields were classified by crop residue type and selected randomly each year. Field edges were selected randomly within fields. Only one transect was conducted per field in a given year. Subsequent transects were located at least 150 m apart to ensure independence. Surveys were conducted in February each year between sunrise and 11:00 EST on mornings with no precipitation and wind less than 25 kmph. We surveyed both field border and control farms on the same days and alternated which treatment was surveyed first.

Field edges were surveyed with a strip transect method. Each strip was 10 m wide, corresponding to the maximum width of the field borders. On control farms, a corresponding 10 m of crop residue and mowed vegetation was surveyed. The observer walked along the field edge and counted all birds within the 10 m strip. When flushed, sparrows tended to fly along the field edge and land in the vegetation farther down the border. The location of these birds was noted and a bird subsequently flushed was not counted a second time.

Because it was possible for birds to escape detection within field borders, the probability of detecting a bird was estimated by having a field assistant walk through the middle of the field border immediately after the observer finished the transect and flush all remaining birds in the strip by shouting and beating the vegetation. This was repeated for 31 transects. A detection probability was calculated by dividing the number of birds counted by the observer by the total number of birds detected (Lancia et al. 1994). We assumed that the field assistant flushed all birds remaining in the strip. Any violation of this assumption would yield a lower density estimate in field borders. The probability of detecting a bird in a mowed edge was assumed to be 1 because of the lack of vegetation in mowed edges. For the few mowed edges that contained a substantial amount of cover, a field assistant was used in the manner described above to ensure that all birds were counted.

Sparrows were not identified to species during surveys because of the difficulty of observing subtle field marks while maintaining an accurate count of the number present. Relative species composition of sparrows in field edges was estimated by identifying birds while walking between a random subset of transect starting points. Approximately 4.5 h was spent identifying 149 birds in field borders and approximately 1.5 h was spent identifying 22 birds in mowed edges. To avoid the bias of overcounting species that are readily identified from a distance [e.g., Dark-eyed Junco (*Junco hyemalis*)], only observations of perched or standing sparrows made through binoculars were included.

Field interiors were surveyed by walking transects through the middle of fields (45–50 m from field edges in Hyde County and 35–55 m from field edges in Wilson County). The perpendicular distance from the transect line to each individual or cluster of birds was estimated.

Transect lengths were measured with a range finder or by pacing. To avoid observer bias in estimates of distance and flock size, a single observer conducted all surveys.

We conducted 72 strip transects averaging 0.30 ± 0.02 km on field borders and 66 strip transects averaging 0.27 ± 0.02 km on mowed edges ($\bar{x} = 0.22$ km in Wilson County and 0.38 km in Hyde County). We conducted 62 line transects averaging 0.28 ± 0.03 km on field interiors with field borders and 62 transects averaging 0.26 ± 0.02 km on fields with mowed edges ($\bar{x} = 0.19$ km in Wilson County and 0.43 km in Hyde County).

Data analysis.—Counts of sparrows in field edges were adjusted for detectability by dividing by the detection probability. These adjusted counts were converted to densities by dividing the adjusted count by the area surveyed for each transect.

In field interiors, sparrows could easily hide in the crop residue and the probability of detecting a sparrow decreased as a function of distance from the survey line. To obtain density estimates, field interior observations were treated as line transect surveys and densities were estimated by fitting a detection function to the data (Buckland et al. 1993) in program DISTANCE (Laake et al. 1993). If sparrows were not randomly distributed on fields and preferred to forage near field edges (Pulliam and Mills 1977, Lima 1990, Lima and Valone 1991, Watts 1991), then densities in field interiors may have been underestimated because sparrow detectability was lowest toward the field edge. It was necessary to pool all transects within treatments to obtain sufficient sample sizes for the program DISTANCE, which diminished our power to discriminate differences between treatments and test for year effects. To compare treatments (i.e., field borders or mowed edges) for field interior surveys, we created an index of abundance by summing all sparrows detected within 50 m of the transect line and dividing the count by the area surveyed for each transect.

Sparrow abundance data for both field edges and interiors were averaged within year, site, and treatment. This design yielded 16 estimates of mean sparrow abundance on field edges and interiors for each farm. Average sparrow abundances were log-transformed because variances were correlated to means. Multivariate homogeneity of variances was tested using a Sen-Puri's test ($\chi^2 = 28.4$, 21 df, $P > 0.05$; StatSoft 1995). Bartlett χ^2 univariate tests of homogeneity of variances for log-transformed mean sparrow densities along field edges ($\chi^2 = 4.5$, 7 df, $P > 0.05$) and sparrow abundance in field interiors ($\chi^2 = 8.5$, 7 df, $P > 0.05$) were not significant (StatSoft 1995). Differences in sparrow abundance on farms with and without field borders were determined from a 3-way MANOVA (StatSoft 1995) with year, treatment, and site as factors. Dependent variables were transformed average sparrow densities for field edges and sparrow abundance for field interiors. Post-hoc comparisons were conducted using Tukey's HSD (StatSoft 1995). Relative proportions of sparrow species were compared using log-linear analysis and Freeman-Tukey deviates (StatSoft 1995). Analyses were conducted using StatSoft version 5.1 for the PC.

RESULTS

Most (93%) birds detected in field edges were sparrows. The remaining 7% consisted primarily of Northern Cardinals (*Cardinalis cardinalis*), American Robins (*Turdus migratorius*), and Yellow-rumped Warblers (*Dendroica coronata*). Of 127 sparrows positively identified in Wilson County, 50% were Dark-eyed Juncos, 24% were Song Sparrows, 15% were White-throated Sparrows (*Zonotrichia albicollis*), 6% were Savannah Sparrows, 3% were Field Sparrows, and 1% were Chipping Sparrows (*Spizella passerina*). Of 44 sparrows positively identified in Hyde County, 50% were Song Sparrows, 36% were Savannah Sparrows, and 14% were Swamp Sparrows (*Melospiza georgiana*). Sparrow species were not distributed randomly with respect to treatment ($\chi^2 = 52.44$, 6 df, $P = 0.001$). Seven species of sparrows were identified in field borders and four species were found in mowed edges. The species detected only in field borders and not in mowed edges were Field, Chipping, and White-throated sparrows. We observed a greater proportion of the Dark-

TABLE 1. MANOVA results for effects of treatment, year, and site on sparrow abundance.

Source[a]	Wilke's λ	Rao's R	Num df	Den df	P
Year	0.41	5.04	2	7	0.044
Site	0.63	2.05	2	7	>0.05
Treatment	0.22	12.17	2	7	0.005
Year × Site	0.63	2.05	2	7	>0.05
Year × Treatment	0.36	6.11	2	7	0.029
Site × Treatment	0.77	1.06	2	7	>0.05
Year × Site × Treatment	0.61	2.23	2	7	>0.05

[a] Year = 1997 vs 1998, Site = Wilson vs Hyde County, Treatment = field borders vs mowed edges.

eyed Juncos in field borders and a greater proportion of Savannah Sparrows in mowed edges.

The probability of detecting a sparrow in a field border was 0.71 ± 0.081. Sparrow abundance was greater on farms with field borders than with mowed edges during our sampling period (Table 1). However, the significant interaction between year and treatment indicates considerable variation in sparrow abundance on farms with mowed edges between years. Sparrow abundance was greater on farms with mowed edges in 1998 than 1997. In field edges, differences in sparrow densities by treatment were noticeably more pronounced in 1997 than 1998. Contrasts indicated that the significant treatment effects from the MANOVA were due to higher sparrow densities in field edges ($F = 19.29$, 1 df, $P = 0.002$), but not field interiors ($F = 0.14$, 1 df, $P > 0.05$). Sparrow abundance did not differ between sites (Table 1).

In 1997 we detected 33.47 ± 9.5 sparrows/ha in field borders and 5.76 ± 1.7 sparrows/ha in mowed edges. In 1998 we detected 35.69 ± 7.9 sparrows/ha in field borders and 20.90 ± 7.7 sparrows/ha in mowed edges. For both years combined we detected 34.52 ± 6.2 sparrows/ha in field borders and 12.87 ± 3.8 sparrows/ha in mowed edges. In field interiors we detected 8.90 ± 2.7 sparrows/ha in fields surrounded by field borders and 3.93 ± 1.7 sparrows/ha in fields surrounded by mowed edges for both years combined. In field interiors, mean cluster size of sparrows in Wilson Coun-

TABLE 2. Means (SE) of vegetative structure measurements of field edges, with and without field borders, in Hyde and Wilson counties, North Carolina.

Measurement	Wilson Co. Field border	Wilson Co. Mowed edge	Hyde Co. Field border	Hyde Co. Mowed edge
Feb. 1997 & 1998				
% Cover[a]	92.3 (2.1)	15.2 (3.4)	74.5 (2.8)	4.1 (1.5)
Median ht. in m[b]	1.12 (.04)	0.48 (0.08)	0.90 (0.05)	0.18 (0.05)
Summer 1997				
Vertical structure[c]	38.9 (2.6)	20.7 (2.4)	22.9 (3.6)	4.6 (3.5)
Bare ground[d]	5.8 (4.2)	21.7 (3.9)	5.0 (5.8)	70.4 (5.6)
Grasses[e]	50.6 (4.9)	49.6 (4.6)	20.5 (6.8)	19.0 (6.5)
Forbs[f]	50.4 (4.3)	39.5 (3.9)	39.5 (5.9)	9.9 (5.6)
Woody[g]	19.0 (2.6)	6.5 (2.4)	5.9 (3.6)	0
Food plants[h]	3.6 (0.5)	2.6 (0.5)	2.3 (0.7)	0

[a] Visual estimate of the percentage of the 10 m strip of field edge that contained standing vegetation over 15 cm.

[b] Visual estimate of median height of standing vegetation.

[c] An index of structure, derived from averaging 5 measurements on density pole.

[d] % cover of bare ground accessible to a sparrow.

[e] % cover of grasses, includes grasses, sedges, and rushes.

[f] % cover of all broad leafed, non-woody vegetation.

[g] % cover of all woody plants.

[h] Index of potential winter food plants, derived from Judd 1901, Martin et al. 1951, Pulliam and Enders 1971, and pers. obs. Index is average of percent coverages for panicum (*Panicum* sp.), ragweed (*Ambrosia artemisiaefolia*), lambsquarter (*Chenopodium album*), dock (*Rumex* sp.), lespedeza (*Lespedeza* sp.), and blackberry (*Rubus argutus*).

TABLE 3. Comparison of wintering sparrow densities on agricultural lands. Note that different methods were used to derive density estimates, and surveys were conducted in different months.

Density (sparrows/ha)	Species	Habitat	Location	Reference
0.0–1.5	Am. Tree Sparrow (*Spizella arborea*)	CRP fields	Nebraska	King and Savidge (1995)
0.1–12.2	Savannah Sparrow	Grasslands	Oklahoma and Texas	Grzybowski (1983)
0.4	Am. Tree and Song sparrows and Dark-eyed Junco	CRP fields	Missouri	Best et al. (1998)
1.1	Am. Tree and Song sparrows and Dark-eyed Junco	Rowcrop fields	Missouri	Best et al. (1998)
3.9	Mostly Savannah Sparrow and Dark-eyed Junco	Rowcrop fields w/out field borders	North Carolina	This study
4.6	Mostly Am. Tree Sparrow	Hedgerows	New York	Petrides (1942)
8.9	Mostly Savannah Sparrow and Dark-eyed Junco	Rowcrop fields w/field borders	North Carolina	This study
12.9	Mostly Savannah and Song sparrows	Mowed field edges	North Carolina	This study
13.4	Savannah and Song sparrows	Mowed, abandoned fields	Georgia	Watts (1990)
14.7	Savannah and Song sparrows	Unmowed, abandoned fields	Georgia	Watts (1990)
26.6	Savannah and Song sparrows	Open[1] old fields next to plowed fields	Georgia	Watts (1996)
34.5	7 sparrow species[2]	Field borders	North Carolina	This study
110.8	5 sparrow species[3]	Open[1] old fields adjacent to brambles	Georgia	Watts (1996)
115.8	Savannah and Song sparrows	Weedy[4] old fields next to plowed fields	Georgia	Watts (1996)
189.1	5 sparrow species[3]	Weedy[4] old fields adjacent to brambles	Georgia	Watts (1996)

[1] Open old fields were 2–6 year old fallow fields with low forb density.
[2] Savannah, Song, Swamp, White-throated, Field, Chipping sparrows and Dark-eyed Juncos.
[3] Savannah, Song, Swamp, White-throated, and Field sparrows.
[4] Weedy old fields were 2–6 year old fallow fields with high forb density.

ty (5.50 ± 1.24 sparrows/cluster) was larger ($Z = 3.22$, $n = 203$, $P < 0.002$) than in Hyde County (1.49 ± 0.12 sparrows/cluster). The cluster size of sparrows we observed in field interiors with mowed edges (4.22 ± 0.38 sparrows/cluster) was larger ($Z = 1.98$, $n = 203$, $P = 0.048$) than in field interiors with field borders (2.06 ± 1.02 sparrows/cluster).

In both winters, field borders had more and taller vegetative cover than mowed edges (Table 2). Vegetative cover and height in field borders and mowed edges were similar between years on all farms, except for Hyde County, where field borders had 85% mean cover in 1997 and 61% in 1998. In the summer of 1997, vegetation in field borders was taller and had more vertical structure and potential food plants than existed in mowed edges. Wilson County field edges contained more vegetative cover than Hyde County field edges (Table 2).

DISCUSSION

Several mechanisms may be responsible for the greater densities of sparrows found on farms with field borders. Field borders might provide better escape cover than mowed edges. Several researchers suggested that sparrows prefer to forage near cover to reduce the risk of avian predation (Schneider 1984, Lima

1990, Watts 1990). Lima (1990) found that White-crowned Sparrows (*Zonotrichia leucophrys*) foraged only near cover even when food was abundant farther from cover. He surmised that this was due to predation risk. We often observed sparrows flying to field borders, wood piles, or adjacent timber stands when disturbed in fields. Because the value of escape cover may be limited by distance (Watts 1991), the presence of field borders in the middle of large farmed openings may make more of the farm landscape available to sparrows (Petrides 1942), particularly for shrub dependent species (Lima and Valone 1991). Field border vegetation also may increase food resources for sparrows, as indicated by the greater amounts of potential winter food plants found in field borders (Table 2). Additionally, field borders may provide thermal protection for sparrows (Grubb and Greenwald 1982).

Wintering sparrow densities vary widely in agricultural landscapes (Petrides 1942, Grzybowski 1983, Watts 1990, King and Savidge 1995, Watts 1996, Best et al. 1998). The sparrow densities we recorded for fields and mowed edges were similar to, and densities in field borders greater than, densities reported in most studies. This suggests that agricultural fields with field borders may provide good wintering habitat for sparrows (Table 3). However, caution should be exercised when comparing densities between studies, because different methodologies were used and species composition differed.

We expected sparrow densities to differ between Wilson and Hyde counties because field border vegetation was taller and denser in Wilson County. Moreover, Wilson County fields were closer to other suitable habitats, such as timber, abandoned house sites, and other uncultivated areas. We had anticipated that juxtaposition of these habitat features would allow more sparrows to take advantage of fields and field borders but this was not observed.

The larger mean cluster size in field interiors with mowed edges may have been a response to increased perceived predation risk (Barnard 1980). Sparrows also may have been concentrated because less suitable foraging habitat was available on fields with mowed edges. The smaller mean sparrow cluster size we observed in Hyde County field interiors may be due to the higher proportion of Savannah Sparrows, which tended to be solitary or form looser flocks than other sparrows.

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BIRD NESTING ECOLOGY IN A FOREST DEFOLIATED BY GYPSY MOTHS

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ABSTRACT.—Acadian Flycatcher (*Empidonax virescens*, $n = 55$), Indigo Bunting (*Passerina cyanea*, $n = 60$), Eastern Towhee (*Pipilo erythrophthalmus*, $n = 41$), and Wood Thrush (*Hylocichla mustelina*, $n = 62$) nests were monitored during 1995–1996 in the eastern panhandle of West Virginia, at the Sleepy Creek Wildlife Management Area. The objective of this study was to relate the outcomes of bird nests to surrounding habitat characteristics in an area that experienced heavy tree mortality from prior defoliation by the gypsy moth (*Lymantria dispar*). Large (> 22.9 cm dbh) standing snags in the nest patch were not associated with nest failure for any of the four bird species. Very large diameter (> 38.1 cm dbh) live trees and snags and reduced canopy cover increased the chances of Brown-headed Cowbird (*Molothrus ater*) parasitism only for Indigo Buntings. Nest patches of all four species differed in vegetation characteristics from random plots in similar habitat, typically by having greater densities of species' preferred nesting substrate in the nest patch. Gypsy moth defoliation, which can result in an increase in snags and opened canopy, is not likely to be a devastating ecological event for shrub and sub-canopy nesting avian species, and can create more nesting habitat for many species that use a dense forest understory. *Received 18 Jan. 2000, accepted 22 June 2000.*

The gypsy moth (*Lymantria dispar*) was introduced to North America around 1869 and has become an important forest pest in the eastern United States (Liebhold 1990). Gypsy moth defoliation alters the structure and composition of the forest by causing tree mortality (Campbell and Sloan 1977, Houston and Valentine 1977, Bell 1997). Oaks (*Quercus* spp.) in particular are a preferred food item in the East (Twery 1991, Liebhold et al. 1995). To limit both the spread and the damage caused by gypsy moths, spraying of pesticides, primarily *Bacillus thuringiensis* and diflubenzuron, has been widespread. Both *Bacillus thuringiensis* and diflubenzuron have detrimental effects on birds (Cooper et al. 1990, Rodenhouse and Holmes 1992, Sample et al. 1993a, Whitmore et al. 1993) through the reduction of non-target Lepidoptera larvae (Sample et al. 1993b, Sample et al. 1996, Butler et al. 1997), an important food source during the breeding season.

Knowing that pesticide use is detrimental to bird populations, it is equally important to assess the possible deleterious effects of inaction on forest birds; that is, when no efforts are taken to control gypsy moth populations and they are left to run their course. Following a heavy gypsy moth outbreak, populations of many ground, shrub, subcanopy, and snag-using bird species increased (Bell 1997, Bell and Whitmore 1997a). However, the relationship between density of a species and the quality of the habitat is not always clear. In some cases, high animal densities indicate high quality habitat and in other cases they do not (Vickery et al. 1992, Van Horne 1983, Hunt 1996, Holmes et al. 1996). In avian conservation, it is necessary to determine which habitat characteristics affect survival and nesting success (Martin 1992), particularly in light of concerns about population declines of many species of migratory landbirds (Robbins et al. 1989, Askins et al. 1990).

There has been speculation that the opening of the forest canopy and the presence of snags, features created by gypsy moth damage, can create conditions favorable for Brown-headed Cowbird (*Molathrus ater*) parasites and nest predators (Robbins 1979, Yahner and Wright 1985, Thurber et al. 1994, Rotenberry et al. 1995). Snags may provide perch sites from which cowbirds could locate nests in which to lay their eggs. It also is possible that avian predators could use them to search for nests. However, in forested landscapes, some researchers have found no relationship between number of snags surrounding the nest patch and parasitism (Brittingham and Temple 1996).

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It is necessary to monitor nests in order to better understand the dynamics of bird nesting ecology in a defoliated forest. In this study we focused on four bird species common to the study area: Acadian Flycatchers (*Empidonax virescens*), Indigo Buntings (*Passerina cyanea*), Eastern Towhees (*Pipilo erythrophthalmus*), and Wood Thrushes (*Hylocichla mustelina*). Numbers of Indigo Buntings, Eastern Towhees, and Wood Thrush increased after gypsy moth defoliation and tree mortality, while Acadian Flycatchers declined (Bell 1997, Bell and Whitmore 1997a, Bell and Whitmore 1997b). Our objectives were to describe the nest-site characteristics of birds in a gypsy moth-impacted forest and to determine which habitat features (if any) differed between parasitized and unparasitized nests, successful and unsuccessful nests, and nest patches and random patches in similar habitat.

STUDY AREA AND METHODS

This study was conducted within the Sleepy Creek Wildlife Management Area (WMA; formerly Sleepy Creek Public Hunting and Fishing Area; 39° 44′ N, 78° 18′ W), an 8000 ha area located on Sleepy Creek and Third Hill Mountains (elev. 240–662 m) in Morgan and Berkeley counties, West Virginia. This study was designed to be mensurative (as opposed to manipulative) in that plots were established to compare experimental units over space or time (Hurlburt 1984, Cooper et al. 1999). We did not believe that comparing nests at Sleepy Creek WMA to undefoliated control sites was feasible. To prevent gypsy moth defoliation and subsequent tree mortality, agents such as *Bacillus thuringiensis* and Dimilin, both of which have been shown to have adverse effects on songbirds would have to be used. To establish plots in areas far enough away from Sleepy Creek WMA so as to be totally unaffected by gypsy moths would introduce site biases in vegetation structure and composition and their concomitant bird faunas.

The Sleepy Creek WMA area lies within the rolling Ridge and Valley province and is typical of the oak-hickory forests of the region. Tree species common to the area include red, chestnut, and white oaks (*Quercus rubra, Q. prinus, Q. alba*), hickories (*Carya* spp.), yellow poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), black birch (*Betula lenta*), sassafras (*Sassafras albidum*), black gum (*Nyssa sylvatica*), and pitch pine (*Pinus rigida*). Sleepy Creek WMA is maintained by the West Virginia Division of Natural Resources and no efforts were taken during this study to control gypsy moth populations in our study plots. Heavy defoliation occurred in 1987 and 1988 as gypsy moth populations reached outbreak levels (Cooper et al. 1993, Bell 1997) and defoliation levels fluctuated after that (Bell 1997). Bird populations and habitats were monitored before (1984–1986), during (1987–1988), and after (1989–1996) the initial severe outbreak. During the time nesting birds were monitored (1995–1996), gypsy moth caterpillars were rarely observed and defoliation was negligible. The amount of damage to the area after defoliation varied widely. By the post-outbreak period, some sites within Sleepy Creek WMA lost up to 80% of their pre-defoliation number of large oak trees (the dominant tree in the area) while others were undamaged and increased in the number of large oaks (Bell 1997).

Vegetation sampling.—Seven transects, each 2 km in length, were established at the study site. Two transects were placed along each elevational gradient (ridgetop, mid-slope, and valley) of the eastern slope of Sleepy Creek Mountain to represent a uniform sample of the locations on the mountain. The seventh transect was along the western midslope of Third Hill Mountain, which lies parallel to Sleepy Creek Mountain. Six circular (125 m radius) permanent plots were placed along each transect, for a total of 42 plots. Within every plot, 5 permanent 0.04 ha subplots were placed, for a total of 210 subplots. One subplot was always located at the plot center and one was randomly located within each of the four quadrants of the 125 m plot. These subplots served as a random sample of the vegetation structure and composition of the area. At each subplot, vegetation (e.g., canopy cover, shrub cover, and number, size, and species of trees) was sampled similar to the manner of James and Shugart (1970). There were 5 sampling points in each cardinal direction spaced 2.26 m apart, for a total of 20 sampling points per 0.04-ha subplot. At each sampling point, ground cover and vegetation were recorded using a sighting tube with a wire cross-hair at the end. The observer sighted vertically through the tube, first down, then up, and vegetation that intersected the cross-hairs, from the ground to the top of the canopy, was recorded. First, presence/absence of canopy above 3 m was recorded as total canopy cover. If foliage 0–3 m was intercepted by the cross-hairs, it was recorded by Genus or species and counted as shrub cover. At each sampling point, every intersection of the vegetation with the cross-hair counted as 5%, so values for each variable ranged from 0–100% at each subplot. The number and diameter at breast height (dbh) of each species of tree (any woody plant > 3 m in height) within the subplot were measured using a modified Biltmore stick (James and Shugart 1970).

Nest monitoring.—Nests of four bird species (Acadian Flycatchers, Indigo Buntings, Eastern Towhees, and Wood Thrushes) were located and monitored. These species were chosen because all four were common to the area and it was believed that their nests could be found in large enough numbers for statistical analysis. Areas within and around the 42 plots were searched intensively for nests. All nests found within the study area were monitored every 3–4 days following the protocols of the Breeding Biology Research and Monitoring Database (BBIRD) program (Martin et al. 1996). After each nesting attempt was completed, vegetation was sampled in a 0.04 ha plot (the nest patch) centered on the nest in the same manner as each of the 210 vegetation sampling subplots were measured. Thus, nest patches chosen by birds could be compared with the vegetation structure and composition of the study site. Nest patches also were compared between successful and unsuccessful, and parasitized and unparasitized nests for each of the four species separately.

Statistical analyses.—Nesting success was calculated using the Mayfield method (Mayfield 1961, 1975; Johnson 1979), a procedure with widespread use (Ralph et al. 1993, Martin et al. 1996). For comparison between successful/unsuccessful and parasitized/unparasitized nests, seven habitat variables were chosen based on habitat structural characteristics that could potentially affect nesting success (Anderson and Storer 1976, Martin 1993, Thurber et al. 1994, Brittingham and Temple 1996, Barber and Martin 1997). These were number of live trees (> 3 m tall) in three size-classes (0–7.6 cm dbh, 22.9–38.1 cm dbh, and > 38.1 cm dbh), number of large dead trees in two size-classes (22.9–38.1 cm dbh and > 38.1 cm dbh), percentage cover of overhead canopy (foliage > 3 m in height), and percentage foliage in the shrub layer (0–3 m tall). The same seven variables and five additional variables (percent cover of the five most common non-herbaceous vegetation species in the nest patch shrub layer) were used to determine if there were any differences between nest patches and random plots for each species. Because nests were found in 1995 and 1996, data from vegetation plots from both years were used. Our goal was to determine microhabitat selection, so when comparing nest plots to random plots, we used only plots of the same general habitat type to find out what nest features the birds were choosing within a generally suitable area. These plots were selected by only using vegetation subplots from plots where each species was detected singing in either year of the study (Bell 1997). To determine which vegetation species were most commonly used for nest placement, the number of nests was tallied by vegetation type for each bird species.

To reduce the number of variables we assessed the association between each habitat variable and the dichotomous outcome of a nest in a univariate logistic regression model for each individual bird species. Variables that had a P value of less than 0.25 were retained for use in a stepwise logistic regression model (Hosmer and Lemeshow 1989). Stepwise logistic regression (Hosmer and Lemeshow 1989, Menard 1995, SAS 1995) was used to determine which habitat variables were associated with the dichotomous outcome of a nest. Significance level to stay in the model was $\alpha = 0.05$. Although stepwise procedures may result in an elevated chance of a Type I error, the goal of stepwise procedures was to identify the most parsimonious set of variables that adequately describe the outcome variable (Hosmer and Lemeshow 1989). Furthermore, it has been suggested that larger values of α are reasonable when specific relationships are anticipated *a priori,* as is the case here (Kupper et al. 1976). To avoid problems with collinearity among variables, all independent variables used in each of the models had a Pearson correlation coefficient of less than 0.5. Statistical analyses were performed using The SAS System, Version 6.12 (SAS Institute Inc. 1996).

RESULTS

During the summers of 1995–1996, we found 55 Acadian Flycatcher, 60 Indigo Bunting, 41 Eastern Towhee, and 62 Wood Thrush nests (Table 1). Comparisons of habitat characteristics between parasitized and unparasitized nests of each species revealed that habitat variables differed only for Indigo Buntings. Parasitized Indigo Bunting nests were more likely to have less canopy cover (61 ± 5.2% vs. 72 ± 3.3%, Wald $\chi^2 = 4.51$, $P = 0.03$, odds ratio = 1.39 for a −10% change), more large live trees (> 38.1 cm dbh; 0.9 ± 0.1 vs 0.5 ± 0.1; Wald $\chi^2 = 5.29$, $P = 0.02$; odds ratio = 4.53), and large (> 38.1 cm dbh) snags (0.9 ± 0.2 vs 0.4 ± 0.1; Wald $\chi^2 = 4.30$, $P = 0.03$; odds ratio = 2.14) in the nest patch than unparasitized nests (total nests $n = 60$). Only Wood Thrushes had significant differences in habitat surrounding successful and unsuccessful nests. Successful nests had more foliage cover in the shrub layer (0–3 m) in the nest patch than failed nests (76 ± 3.0% vs 66 ± 3.2%, $n = 62$; Wald $\chi^2 = 4.37$, $P = 0.03$; odds ratio = 1.4 for a +10% change).

All four bird species' nest patches differed in specific habitat characteristics from surrounding similar habitat. Eastern Towhee nest patches were more likely to have more grapevine (*Vitis* spp.) cover (6.0 ± 1.3% vs 3.1 ± 0.4%; Wald $\chi^2 = 7.29$, $P = 0.0069$; odds ratio = 1.6 for a −10% change) fewer 0–7.6 cm dbh saplings (31.7 ± 3.2 vs 44.6 ± 1.4; Wald $\chi^2 = 13.45$, $P < 0.001$; odds ratio = 0.96), and large-diameter (>38.1 cm dbh) live trees (0.7 ± 0.1 vs 1.3 ± 0.1; Wald $\chi^2 = 6.40$, $P = 0.011$; odds ratio = 0.63) than random plots in similar habitat ($n = 421$). Indigo Bunting nest patches were more likely to have more blackberry (*Rubus* spp.; 50.2 ± 3.2 vs 20.9 ± 1.9; Wald $\chi^2 = 36.89$, $P = 0.001$; odds ratio = 1.53 for a +10% change) and hickory shrub cover (8.4 ± 1.0 vs 6.1 ± 0.6; Wald $\chi^2 = 4.48$, $P = 0.0342$; odds ratio = 1.65 for a +10% change) with fewer 0–7.6 cm dbh saplings (21.0 ± 1.8 vs 39.8 ± 2.3; Wald $\chi^2 = 13.11$, $P < 0.001$; odds ratio = 0.96) and large-di-

TABLE 1. Productivity estimates for Acadian Flycatchers (*Empidonax virescens*), Indigo Buntings (*Passerina cyanea*), Eastern Towhees (*Pipilo erythrophthalmus*), and Wood Thrushes (*Hylocichla mustelina*) in a forest defoliated by gypsy moths (*Lymantria dispar*) in West Virginia, 1995–1996.

Variable	Acadian Flycatcher	Indigo Bunting	Eastern Towhee	Wood Thrush
# nests	55	60	41	62
# exposure days	866.5	626	362.5	778
# successful nests	30	33	15	26
# failed nests	25	27	26	36
Mayfield % success	47%	39%	19%	32%
Mayfield daily predation rate	2.8%	4.3%	7.1%	4.6%
# fledglings per successful nest	2.8	2.5	2.7	3.2
# parasitized nests (%)	8 (15%)	18 (30%)	3 (7%)	15 (24%)
# host young fledged in nests with Brown-headed Cowbird nestlings	0	1.8	2.7	2.3
# host young fledged in nests without Brown-headed Cowbird nestlings	2.8	2.8	2.8	3.3
# Brown-headed Cowbird fledglings per successful host nest	0	0.28	0.03	0.13
# Brown-headed Cowbird fledglings per failed host nest	0.12	0.03	0	0

ameter (>38.1 cm dbh) live trees (0.6 ± 0.2 vs 1.4 ± 0.1; Wald $\chi^2 = 7.53$, $P = 0.0061$; odds ratio = 0.53, $n = 261$) Wood Thrush nest patches were more likely to have more canopy cover (88.0 ± 1.3 vs 83.0 ± 0.8; Wald $\chi^2 = 7.24$, $P = 0.0071$; odds ratio = 1.42 for a +10% change), greater witch hazel (*Hamamelis virginiana*) shrub cover (13.3 ± 2.6 vs 6.3 ± 0.6; Wald $\chi^2 = 12.63$, $P < 0.001$; odds ratio = 1.34 for a +10% change), and fewer of the largest live trees (> 38.1 cm dbh; 0.8 ± 0.1 vs 1.2 ± 0.1; Wald $\chi^2 = 7.09$, $P = 0.0078$; odds ratio = 0.67, $n = 442$). Acadian Flycatcher nest patches were more likely to have more witch hazel (15.5 ± 2.3 vs 9.8 ± 1.1; Wald $\chi^2 = 10.95$, $P < 0.001$; odds ratio = 1.44 for a +10% change) and black birch (*Betula lenta*) (9.9 ± 1.6 vs 5.4 ± 0.7; Wald $\chi^2 = 5.55$, $P = 0.0184$; odds ratio = 1.42 for a +10% change) shrub cover, fewer live trees (> 22.9–38.1 cm dbh; 1.9 ± 0.2 vs 2.3 ± 0.2; Wald $\chi^2 = 4.30$, $P = 0.0379$; odds ratio = 0.81) and fewer 0–7.6 cm dbh saplings (42.9 ± 2.4 vs 55.0 ± 2.0; Wald $\chi^2 = 13.29$, $P < 0.001$; odds ratio = 0.97) than random plots ($n = 220$).

Most Acadian Flycatcher nests we found were in witch hazel (42%), followed by red maple (22%), black birch (16%), and dogwood (13%). Eighty percent of Indigo Bunting nests found were in *Rubus* spp. Eastern Towhee nests were primarily found in grapevine (27%), *Rubus* spp. (17%), greenbriar (12%), and mountain laurel (12%). Wood Thrush nests were found primarily in witch hazel (32%), black gum (19%), and red maple (19%).

DISCUSSION

We found no association between large snags in the nest patch and higher nest predation for the four species in this study. We found that Indigo Bunting nests at sites with less canopy cover, but with large diameter trees and snags were parasitized more than nests with a more closed canopy and fewer large-diameter trees and snags. Because this effect was seen with both live and dead trees, the important factor appears to be the size of the tree in an open area, regardless of whether the tree is live or dead. In more open habitat, the presence of emergent live trees has been noted to increase the probability of parasitism (Anderson and Storer 1976, Johnson and Temple 1990). Clearcuts with snags were found to have more Brown-headed Cowbirds than those with no snags (Dickson et al. 1983), further indicating that large trees in open stands may be used by cowbirds. The structure of the understory also may have compounded the perch effect. Eighty percent of the Indigo Bunting nests we found were in blackberry (or in small seedling trees mixed in with blackberry), which is shade intolerant and was found in large canopy gaps on drier sites within the study area. In the canopy gaps where we typically found Indigo Bunting nests, there were significantly fewer small trees than in the surrounding habitat. Thus, either a large diameter snag or live tree, where the canopy was generally open with no subcanopy could provide a good view of the understory where these birds were nesting.

None of the other species we examined had higher parasitism rates when large trees or snags were in the nest patch. As suggested by other researchers (Barber and Martin 1997, Brittingham and Temple 1996), snags may provide a view above the canopy but not below the canopy where nest-building of subcanopy species, such as Wood Thrushes and Acadian Flycatchers occurred. Therefore, a large snag surrounded by a dense subcanopy of saplings may not provide a good nest locating perch for cowbirds.

Habitat characteristics between successful and failed nests were different only for Wood Thrushes. Successful Wood Thrush nests had more foliage cover in the shrub layer (cover 0–3 m high) in the nest patch than failed nests. Wood Thrush nests are bulky compared to many passerine nests and when placed in an understory sapling tree are often visible to humans and possibly to potential predators. Dense foliage cover in the nest patch of a Wood Thrush nest may lessen the chances of detection by predators by obscuring it or decreasing scent transmission.

Acadian Flycatchers and Wood Thrushes placed most of their nests in witch hazel. This low spreading shrub provides nest placement sites and adequate concealment. Both species' nests were found in areas with a closed canopy (approximately 88% closure) and shade tolerant witch hazel in the understory. Although successful nests did not differ from failed nests in the amount of shrub level witch hazel, nest patches for both species had significantly more witch hazel cover in the shrub layer than random vegetation plots. A similar pattern was seen for Indigo Buntings and Eastern Towhees, both of which had significantly more foliage cover of their preferred nesting substrate (*Rubus* spp. and *Vitis* spp. respectively) in the nest patch than did random vegetation plots. That birds had more of the plants they chose for nesting in the nest patch than nearby random patches provides support for the idea that birds may select nest patches with more potential nest sites in order to reduce predator search efficiency (Martin 1993, Farnsworth and Simons 1999).

Three of the four species we examined had significantly fewer saplings in the nest patch than in the surrounding habitat. Indigo Bunting and Eastern Towhee nests were primarily found in vining plants [e.g., greenbriar (*Smilax* spp.), grapevine, Virginia creeper (*Parthenocissus quinquefolia*)] or in spreading shrubs such as blackberry, mountain laurel (*Kalmia latifolia*), spicebush (*Lindera benzoin*), and azalea (*Rhododendron* spp.). A dense stand of saplings creates a more closed canopy that would inhibit the shrubby growth used by Indigo Buntings and Eastern Towhees for nesting, further indicating that not all types of early successional habitat are equally suitable for bird species considered early successional (Bell and Whitmore 1997b). Although Acadian Flycatchers used saplings for nesting, their nest patches also had significantly fewer sapling trees than surrounding habitat. Acadian Flycatchers prefer areas with a more open understory (Johnston 1970, Gates and Giffen 1991), possibly because of their aerial foraging (Ehrlich et al. 1988) or aerial nest defense (Wilson and Cooper 1998a). This species declined after gypsy moth outbreak (Bell 1997), possibly because of increased numbers of small trees in the mesic habitat they preferred. That Acadian Flycatchers choose nest sites with fewer small trees lends support to the idea that increased understory cover may have made the area less suitable for Acadian Flycatchers. It is possible that their numbers decreased because of the presence of gaps in the canopy, although no differences were found in the amount of canopy cover or the largest live trees and snags between nest plots and random plots in similar habitat.

Habitat features related to the probability of parasitism and predation differed among the four species we examined. Our results suggest that species should not be pooled when examining the probability of parasitism and predation associated with habitat (see also Brittingham and Temple 1996). Even species with seemingly similar nest sites, such as Eastern Towhees and Indigo Buntings showed differences in habitat features related to predation and parasitism; pooling might mask these differences.

It is possible that landscape factors may influence success rates more than defoliation induced habitat changes. According to U.S. Forest Service FIA (Forest Inventory and Analysis) data, Morgan and Berkeley counties in West Virginia, where the Sleepy Creek WMA is located, are approximately 62% forested cover. Areas near Sleepy Creek and Third Hill mountains are even more densely forested. The study plots, although located in a large forested tract, are situated near the periphery of the Sleepy Creek WMA. While they are in the forest interior (> 250 m from edge, based on Robinson et al. 1995), they are within 1.7–7.0 km of agricultural land and human development; cowbirds were heard in the vicinity of all the study plots. Parasitism rates for the species we studied at Sleepy Creek WMA are generally lower than has been reported elsewhere (Walkinshaw 1961, 1966; Brittingham and Temple 1983; Burhans 1997; Suarez et al. 1997; Wilson and Cooper 1998b); however, this may be in part a reflection of a trend for lower parasitism in the East (Hoover and Brittingham 1993). It may also be due to the relatively high percentage of forest cover in the region and closely surrounding the study area, as well as the large size of the study area. Predation and parasitism results at Sleepy Creek were similar to what Robinson and coworkers (1995) found for sites in the Midwest with surrounding forest cover of 60–80%. The exceptions are that Indigo Buntings at Sleepy Creek had slightly higher percent parasitism than was found for heavily forested areas in the Midwest (Robinson et al. 1995). Wood Thrushes had slightly higher daily predation rates and slightly lower percent parasitism and Acadian Flycatchers had lower daily predation rates. The Mayfield nest success rate for Indigo Buntings at Sleepy Creek WMA was higher than was found in riparian habitat in Iowa (Best and Stauffer 1980), and was comparable to that found in several types of gradual edge habitat (stream openings, selection cuttings) in southern Illinois (Suarez et al. 1997). In treefall gaps Suarez and coworkers (1997) reported higher Mayfield nest success in addition to higher percent parasitism for Indigo Buntings than we found, even though all Indigo Bunting nests at Sleepy Creek WMA were in canopy gaps. The Mayfield success rate for Wood Thrushes at Sleepy Creek WMA was lower than rates reported by Hoover and coworkers (1995) for large forested tracts (>100 ha), and comparable to what they found in smaller forest fragments (< 80 ha). However, nesting success of Wood Thrushes in Great Smoky Mountains National Park (Farnsworth and Simons 1999) was found to be similar to what we found at Sleepy Creek WMA. Without data on nesting success prior to defoliation, we are unable to determine if success rates or percent parasitism changed after defoliation.

Tree mortality ranged from approximately 0% to greater than 70% at stands within the study site, with losses on the average of 40% (Bell 1997). Tree losses greater than 50% are considered catastrophic, but generally only 10–15% of infested stands have such high tree mortality (Gottschalk 1991). Considering that losses of less than 20% are most common (Gottschalk 1991), gypsy moth defoliation is not likely to be a devastating ecological event for shrub and sub-canopy nesting species. In light of evidence that many species of birds that use early-successional habitat are declining (Hagan et al. 1992, Hagan 1993, Litvitis 1993, Askins 1995), gypsy moth defoliation and concomitant tree mortality might be useful in creating more nesting habitat for many species that use shrubs and small trees.

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Behavior of Post-nest Failure and Non-breeding Common Loons During the Breeding Season

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ABSTRACT.—Common Loon (*Gavia immer*) breeding, pre-migratory, and wintering behavior has been well described, but no previous author has characterized failed and non-breeding loon behavior during the summer breeding season. We quantified the summer behavior of non-breeding and failed breeding loons from 15 lakes in Kejimkujik National Park (Nova Scotia, Canada) and the Lepreau watershed (New Brunswick, Canada). Time-activity budgets and event quantifications were used to describe behavioral state and event patterns. The behavior of failed and non-breeders in summer is similar to that described for pre-nesting, pre-migratory, wintering, and breeding loons (except those with young chicks) with foraging the predominant behavior and peering the predominant event. We propose that the behavioral regimen of adult loons is relatively constant throughout the year, with the exception of a two-week period following chick hatching when adults brood their young. *Received 16 Dec. 1999, accepted 16 August 2000.*

Common Loon (*Gavia immer*) breeding behavior has been well described (Sjölander and Ågren 1972, McIntyre 1975, Evers 1994), as has the behavior of pre-migratory (McIntyre and Barr 1983) and wintering loons (McIntyre 1978, Daub 1989, Ford and Gieg 1995). However, no previous researcher has quantified the behavior of failed or non-breeding loons during the summer. The paucity of such data was acknowledged by Evers (1994) when he considered what the time distribution of loon pairs without breeding duties might be. Evers (1994) compared his pre-nesting behavioral catalogues to the fall and winter catalogues described by other researchers (e.g., McIntyre 1978, McIntyre and Barr 1983) and showed that foraging comprised 50–60% of behavioral activity. The question remained whether this would be true for non-breeding loons during the summer. As part of a larger study, we examined the summer behavior of non-breeding and failed breeding loons at two sites in Atlantic Canada. The results allow for a more complete description of the annual behavior of non-breeders and for those that lost their nest.

Between 1996 and 1997, 47 pairs of resident Common Loons in Kejimkujik National Park, Nova Scotia, Canada (44° 20′ N, 65° 20′ W) and the Lepreau watershed, south-western New Brunswick, Canada (45° 20’ N, 66° 35’ W) were selected during the spring pre-nesting season. We had no way of *a priori* selecting lakes or pairs that would or would not breed. Twenty-one pairs did not subsequently breed and we continued monitoring 14 of those pairs for the duration of the summer. Six pairs bred but failed early in incubation; we continued monitoring four of those pairs for the duration of the summer. The 14 non-breeding and 4 failed breeding pairs that we monitored resided on 15 lakes with varied lake chemistry, lake morphometry, and biological characteristics. Most of our study lakes were small (<100 ha) single pair territories, with only three lakes having more than one pair.

All observations were made with 8×42 binoculars and/or a 20–60× spotting scope, from a concealed location, between 1 May and 1 September, 1996 and 1997 for a total of 75 h of randomly distributed diurnal observation (n = 108 observations, mean observation time = 41.7 min per bout, range = 11–120 min per bout). Only one randomly chosen individual of any pair was watched during an observational bout. Individuals were only identified to known residential pairs because many of the study subjects were unbanded and identifica-

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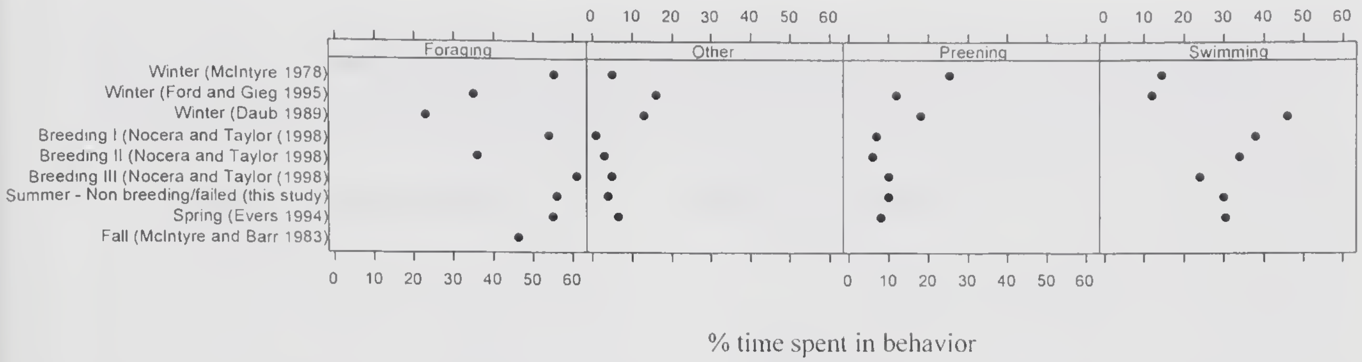

FIG. 1 Comparison of seasonal behavior descriptions for Common Loons. Categories of Breeding (Nocera and Taylor 1998) are: I = adults with chicks 14+ days old, II = adults with chicks 1–14 days old, III = nonincubating member of a nesting pair.

tion of unmarked individuals is often impossible.

We catalogued behavioral states (any behavior typically lasting longer than 5 s; Martin and Bateson 1993) of non-breeding and failed breeding loons using time-activity budgets. Time-activity budgets are commonly used to quantify the proportion of time that an individual spends in various behavioral states (Altmann 1974). We quantified event behaviors (any behavior typically lasting less than 5 s; Martin and Bateson 1993) to take into account subtler behaviors that are often overlooked in time-activity budgets. Behavioral states were categorized as swimming (including drifting), preening, and diving. Territorial encountering, bill tuck, and bathing were summed as "other"; these behaviors were rarely observed. Behavioral events included foot-waggling, stretching, vulture-posturing, splash-diving, peering, yawning, vocalizing (wails, tremolos, hoots, yodels and mews), penguin-dancing, and rushing (Sjölander and Ågren 1972, McIntyre 1975). Peering sometimes lasted longer than 5 s, but rarely exceeded 15 s. Thus, peering was classified as an event for the purposes of this investigation.

Non-breeding loons and loons with failed nests at both sites predominantly spent their time foraging (56%), followed by swimming (30%), preening (10%), and other activities (4%). All event behaviors occurred at least once; the predominant event was peering (19.2 events per h), followed by tremolo vocalization (4.2 per h); stretching and foot waggling were equally common (3.0 per h). All other event behaviors were relatively rare (<1.0 event per hour).

We detected few differences between behavioral catalogues of failed and non-breeders and those published of pre-nesting, breeding, post-nesting pre-migratory, and wintering loons (Fig. 1). The time-activity budget hierarchy we observed is similar to that described by McIntyre (pers. comm., 1978) for wintering loons (foraging > preening > swimming > other). McIntyre and Barr (1983) did not report complete time-activity budgets for loons on autumnal staging grounds, but they noted foraging as the predominant behavioral state. The spring time-activity budgets described by Evers (1994) were analogous to those of our study. Ford and Gieg (1995) reported wintering loons spent most of their time foraging, followed by swimming, preening and other, which again resembles failed and non-breeding loon behavioral patterns in summer. However, Daub's (1989) designation of swimming and drifting as the predominant wintering state differs from our results.

Likewise, certain groups of breeding adults on our study lakes (Nocera and Taylor 1998) exhibited the same hierarchy (Fig. 1). The similarities to breeding loons are limited to non-incubating members of a nesting pair and adults with more developed young (> 14 d old), whereas the behavioral hierarchy of breeding adults with young chicks (< 14 d old) differs because of the necessity to brood chicks. However, even during this period, foraging was the predominant behavioral state (36%), followed by swimming (34%), with brooding (21%) as the third most common behavior.

Evers (1994) found that pre-nesting loons spent 53–57% of their time foraging, 29–32% swimming (sum of resting and locomotion), 8% preening, and 4–5% other. Those results are almost identical to the percentages we found for failed and non-breeders (56%, 30%, 10%, and 4% respectively; Fig. 1). Our results differ from the wintering behavioral patterns described by Daub (1989) who found that drifting (equivalent to our designation of swimming) was the predominant behavior with less time devoted to foraging. One source of discrepancy may be that Daub (1989) used instantaneous sampling [as did Ford and Gieg (1995)], whereas we used continuous sampling. Instantaneous sampling may not offer the sensitivity necessary to accurately describe activity patterns of animals (Martin and Bateson 1993).

The strong similarities between the time-activity budgets of wintering, pre-migratory, pre-nesting, nesting, post-hatch (with chicks older than 14 d), and failed and non-breeding loons seem initially counter-intuitive because of habitat differences. Evers' (1994) study site at Seney National Wildlife Refuge in Michigan consisted of shallow, eutrophic pools with few shoreline irregularities, while the wintering studies occurred at sea under variable conditions (McIntyre 1978, Daub 1989, Ford and Geig 1995). Lakes in our Atlantic Canada study area tend to be deep and oligotrophic with a high degree of shoreline complexity (Kerekes and Schwinghammer 1973). Additionally, there may be a difference in fish availability between these study sites, which may affect foraging time requirements. We propose that foraging time for adult loons may be limited, but they may vary the intensity of foraging by modifying the time spent submerged. This idea is supported by observations of breeding loons (Nocera and Taylor 1998) that suggest adults with 1–14 day old chicks, spend less time diving and more time swimming.

We previously reported that breeding loons in our study sites exhibited aberrant behavioral patterns associated with increased mercury exposure (Nocera and Taylor 1998). Therefore, the comparison we have made between breeding loons and failed and non-breeders needs to be regarded with caution. However, the behavior of failed and non-breeders was not sensitive to mercury exposure, lake chemistry, lake morphometry, or other select biological characteristics of a territory (Nocera and Taylor 1998).

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Sloths in the Diet of a Harpy Eagle Nestling in Eastern Amazon

Mauro Galetti[1,3] and Oswaldo de Carvalho, Jr.[2]

ABSTRACT.—Prey remains of a nestling Harpy Eagle (*Harpia harpyja*) over 15 months in eastern Amazon, Brazil included 11 two-toed sloths (*Choloepus didactylus*), 9 three-toed sloths (*Bradypus variegatus*), and 1 gray four-eyed opossum (*Philander opossum*). We found no evidence of predation on primates despite their abundance in the area and their importance to Harpy Eagles studied elsewhere. We observed no sloths in 605 km of line transects, a finding that suggests the inadequacy of transect data to estimate prey density for Harpy Eagles. *Received 12 April 2000, accepted 31 August 2000.*

The Harpy Eagle (*Harpia harpyja*) is considered the most powerful raptor in the world (Sick 1997). Harpy Eagles prey upon large vertebrates, including primates, sloths, opossums, coatis, kinkajous, and macaws (del Hoyo et al. 1994). Although Bierregaard (1995) mentions that the Harpy Eagle is one of the most studied Neotropical raptors; there is little information available on its ecology in Brazil (Peres 1990, Galetti et al. 1997, Sick 1997). We present information on the diet based on the prey remains found under a nest in the eastern Amazon, Pará state, Brazil.

We found a Harpy Eagle nest on 21 June 1997 in a 40 m tall legume tree (angelim pedra, *Hymenolobium petraeum*, Leguminosae) at Fazenda Cauaxi, Paragominas (3° 45′ S; 48° 10′ W), Pará, Brazil. The Fazenda Cauaxi is a private farm of about 400 km^2 consisting of a mosaic of pastures, primary forests and selectively logged forests. In June 1997, the nest was occupied by a nestling eagle and an adult Harpy Eagle was observed once about 400 m from the nest. We never observed the adult eagle feeding the juvenile.

We visited the nest of the Harpy Eagle every three months from June 1997 to September 1998. During each visit we collected all available prey remains found under the nest. The bones found under the nest were compared to specimens in the Museu Paraense Emílio Goeldi in Belém, Pará. Our estimate of the number of individuals taken by the Harpy Eagle was based only on the skulls.

Prey remains found under the nest consisted of 21 individuals of 3 species of mammals: 11 skulls of two-toed sloths (*Choloepus didactylus*; body mass = 4.1–8.5 kg), 9 skulls of three-toed sloths (*Bradypus variegatus*; body mass = 2.3–5.5 kg; Emmons & Feer 1997), and 1 gray four-eyed opossum jaw (*Philander opossum*). The sloth skulls found in November and January might have been killed by the young eagle.

Other investigators found frequent use of sloths by Harpy Eagles, but not to the extent we found (Rettig 1978, Izor 1985). Sloths comprised about 36% (Rettig 1978) of the prey items for Harpy Eagles in Guyana. The most intriguing aspect of the eagle's use of sloths is that the two species were taken in similar numbers. Two-toed sloths are mainly nocturnal, while three toed sloths are mainly diurnal (Emmons and Feer 1997, Queiroz 1995); consequently, we would expect three-toed sloths to be taken more frequently than two-toed sloths.

In Guyana, primates (mainly capuchin monkeys, *Cebus* spp.) were the second most frequent item in the diet of Harpy Eagles (Izor 1985). We estimated a density of 22 individuals/km^2 of 5 primate species (*Saguinus midas, Cebus kaapori, Cebus apella, Chiropotes satanas,* and *Alouatta belzebul*) at Fazenda Cauaxi based on line transects. All the primates we observed could be taken by Harpy Eagles and we would expect primates to be the main prey for Harpy Eagles based on their abundance. We never observed sloths in a mammal census in the area (ca 605 km of line transects), indicating the limitation of transect

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censuses to estimate prey density for Harpy Eagles.

Our work shows that at least one pair of Harpy Eagles of the eastern Amazon frequently uses sloths to feed their nestling, even more than observed in Guyana (Rettig 1978, Izor 1985).

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Food Habits of Northern Goshawks Nesting In South Central Wyoming

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ABSTRACT.—Northern Goshawks (*Accipiter gentiles*) nesting in south central Wyoming consumed at least 33 species of prey; 14 were mammals and 19 were birds. Based on percent occurrence in regurgitated pellets, dominant (>10% frequency) prey species included: red squirrel (*Tamiasciurus hudsonicus;* present in 50% of pellets), Northern Flicker (*Colaptes auratus;* 34%), American Robin (*Turdus migratorius;* 30%), golden-mantled ground squirrel (*Spermophilus lateralis*; 27%), and Uinta or least chipmunk (*Tamias spp.;* 10%). Woodpeckers [combined frequency of occurrence for Northern Flicker, Red-naped Sapsucker (*Sphyrapicus nuchalis*), Hairy Woodpecker (*Picoides villosus*), Three-toed Woodpecker (*Picoides tridactylus*), and unknown species] were present in 52% of pellets. Unusual food items in the diet included mule deer (*Odocoileus hemionus*) and American marten (*Martes americana*). *Received 3 March 2000, accepted 17 August 2000.*

Northern Goshawks (*Accipiter gentilis*) eat a diverse diet that varies by region, season, and prey availability (Squires and Reynolds 1997). Goshawk diets are best known for populations nesting in the northwestern (Moore and Henny 1983, Reynolds and Meslow 1984, Bull and Hohmann 1994) and southwestern (Kennedy 1991, Boal and Mannan 1994, Reynolds et al. 1994) United States. Land managers need to understand how goshawk food habits vary across the species' range to render informed management decisions

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(Reynolds et al. 1992). To address this information need, which is particularly lacking for populations nesting in the central Rocky Mountains (Shuster 1980), I examined the food habits of goshawks nesting in south central Wyoming.

METHODS AND STUDY AREA

In 1992, I collected 793 regurgitated pellets from 40 active goshawk nests ($\bar{x}$ = 19.8 pellets/nest) after the young had fledged. All nests were located on the Medicine Bow-Routt National Forest in the Sierra Madre and Medicine Bow Mountain Ranges (2438–3353 m elevation) in south central Wyoming. Dominant tree species in both ranges included lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii;* Marston and Clarendon 1988). Nests were located primarily in lodgepole pine forests with scattered quaking aspen (*Populus tremuloides*, Squires and Ruggiero 1996). Sagebrush grasslands were commonly adjacent to forests on the study area. The climate is montane with precipitation ranging from 81 cm at 2440 m to 122 cm at 3350 m (Marston and Clarendon 1988).

Regurgitated pellets were washed in a fine mesh nylon bag and sorted according to similar hair, bone, and feather fragments. I used xylene to clarify 5–7 guard hairs from each sorted pile to identify prey species based on internal characteristics of the medulla according to Moore and coworkers (1974). I identified feather fragments to order based on node and barb characteristics (Robertson et al. 1984, Brom 1986, Brom 1990) and compared complete feathers and bones to museum specimens at the University of Wyoming for identification to species when possible. Although pellet analysis cannot be used to quantify the number of individuals consumed per prey type (Marti 1987), the technique adequately represents raptor diets (Kennedy 1991, Collopy 1983, Real 1996). Hence, the percent occurrence of prey in the pellets approximates the diet of goshawks nesting on the study area.

RESULTS

Goshawks nesting in south central Wyoming consumed at least 33 species of prey; 14 of these species were mammals and 19 were birds (Table 1). Based on percent occurrence in pellets, dominant (>10% frequency) prey species included: red squirrel (*Tamiasciurus hudsonicus*; present in 50% of pellets), Northern Flicker (*Colaptes auratus;* 34%), American Robin (*Turdus migratorius;* 30%), golden-mantled ground squirrel (*Spermophilus lateralis;* 27%), and Uinta or least chipmunk (*Tamias spp.*; 10%). Woodpeckers [Northern Flicker, Red-naped Sapsucker (*Sphyrapicus nuchalis),* Hairy Woodpecker (*Picoides villosus*), Three-toed Woodpecker (*Picoides tri-*

TABLE 1. Contents of Northern Goshawk pellets (n = 793 pellets collected from 40 nests) from south central Wyoming, 1992.

Prey species	Number (%) pellets with prey item
Mammalian prey	
Red Squirrel (*Tamiasciurus hudsonicus*)	400 (50)
Golden-mantled Ground Squirrel (*Spermophilus lateralis*)	214 (27)
Uinta or Least Chipmunk (*Tamias spp.*)	77 (10)
Deer Mouse (*Peromyscus maniculatus*)	55 (7)
Red-backed Vole (*Clethrionomys gapperi*)	20 (3)
Montane Vole (*Microtus montanus*)	14 (2)
Snowshoe Hare (*Lepus americanus*)	9 (1)
American Marten (*Martes americana*)	3 (<1)
Long-tailed Vole (*Microtus longicaudius*)	3(<10
Long-tailed Weasel (*Mustela frenata*)	2 (<1)
Mule Deer (*Odocoileus hemionus*)	2 (<1)
Western Jumping Mouse (*Zapus princeps*)	2 (<1)
Ermine (*Mustela erminea*)	1 (<1)
Richardson's Ground Squirrel (*Spermophilus richardsonii*)	1 (<1)
Avian prey	
Northern Flicker (*Colaptes auratus*)	270 (34)
American Robin (*Turdus migratorius*)	234 (30)
Black-headed Grosbeak (*Pheucticus melanocephalus*)	18 (2)
Steller's Jay (*Cyanocitta stelleri*)	14 (2)
American Kestrel (*Falco sparverius*)	13 (2)
Red-naped Sapsucker (*Sphyrapicus nuchalis*)	11 (1)
Pine Siskin (*Carduelis pinus*)	7 (1)
Townsend's Solitaire (*Myadestes townsendi*)	6 (1)
Dark-eyed Junco (*Junco hyemalis*)	5 (1)
Evening Grosbeak (*Coccothraustes vespertinus*)	4 (1)
Hairy Woodpecker (*Picoides villosus*)	4 (1)
Pine Grosbeak (*Pinicola enucleator*)	4 (1)
Ruffed Grouse (*Bonasa umbellus*)	4 (1)
Western Tanager (*Piranga ludoviciana*)	4 (1)
Gray Jay (*Perisoreus canadensis*)	2 (<1)
Mountain Bluebird (*Sialia currucoides*)	2 (<1)
Red Crossbill (*Loxia curvirostra*)	2 (<1)
Three-toed Woodpecker (*Picoides tridactylus*)	2 (<1)
Black-billed Magpie (*Pica pica*)	1 (<1)
Unknown Piciformes	119 (15)
Unknown Passeriformes	23 (3)
Unknown Columbiformes	1 (<1)

dactylus), and an unknown Picidae] were present in 52% of pellets. Mammalian remains were found exclusively in only 14% of pellets, while 79% of pellets contained both mammalian and avian remains.

DISCUSSION

Based on the analysis of regurgitated pellets, goshawks nesting in south central Wyoming forage primarily on red squirrels, Northern Flickers, American Robins, golden-mantled ground squirrels, and chipmunks. The degree to which western populations depend on mammalian compared to avian prey varies (Moore and Henny 1983, Boal and Mannan 1994, Bull and Hohmann 1994, Reynolds et al. 1994). Red squirrels are widely distributed throughout North America (Young 1999) and broadly overlap the goshawk's distribution (Reynolds et al. 1992). Limited data indicate that red squirrels are usually present in 5–12% of regurgitated pellets (see Squires and Reynolds 1997: appendix 2). However, I found red squirrels in 50% of pellets suggesting that goshawks nesting in south central Wyoming in 1992 may have preyed on red squirrel more than goshawks in other populations. I found that Northern Flickers accounted for 34% of the diet and Piciformes in general provided 52%. Northern Flickers may be prominent in goshawk diets because their conspicuous markings and behavioral displays attract predators (Grzybowski and Eaton 1976, Reynolds and Meslow 1984, Younk and Bechard 1994). Piciformes, in conjunction with American Robins (30%), accounted for most of the avian prey eaten by nesting goshawks during my study.

Reynolds and coworkers (1992) identified 14 prey species that are particularly important to southwestern populations. All the dominant (>10%) prey of goshawks on this study are included among those 14 species. Thus, although the specific habitat recommendations as discussed by Reynolds and coworkers (1992) for the Southwest may not be directly applicable to lodgepole pine forests in Wyoming, the idea that these prey species should be the focus of habitat management is consistent with my findings.

Five pellets contained prey items that are unusual in goshawk diets; two pellets were composed entirely of mule deer (*Odocoileus hemionus*) hair and three pellets contained American marten (*Martes americana*) hair. Goshawks will feed on mule deer carrion and possibly this accounts for its presence in the pellets (Squires 1995). I also recovered a jaw from a 1–3 week old mule deer from inside an active goshawk nest bowl. Mule deer average about 3.7 kg at birth (Robinette et al. 1973), which is similar in weight to the largest hares killed by goshawks (Kenward et al. 1981). The jaw was fresh and blood stained indicating the fawn had been recently killed or scavenged. There was no tissue present to check for hemorrhaging to determine if the goshawks had killed the fawn or scavenged it. Male martens weigh up to 1250 g (Clark et al. 1987), well within the size class of potential prey that goshawks can kill. I believe this is the first documentation that goshawks may occasionally prey on or scavenge American martens.

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Itinerant Breeding and Mate Switching by an American Dipper

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ABSTRACT.—Several bird species are thought to be itinerant breeders, reproducing in different localities during the same season, but this behavior has been documented conclusively only in the Red-billed Quelea (*Quelea quelea*). In 1997, I observed a case of itinerant breeding and mate switching by a banded female American Dipper (*Cinclus mexicanus*) in western Montana. This female raised a successful first brood on a bridge early in the breeding season, then moved 5 km to a neighboring drainage and successfully raised a second brood in a crevice with a different male. This reproductive behavior may have been facilitated in my study area by the use of low-elevation bridges as nest sites by dippers. *Received 15 Feb. 2000, accepted 22 June 2000.*

Itinerant breeding, or breeding in different localities during the same season, is a reproductive strategy that may increase the overall productivity of certain multi-brooded species, particularly when the food supply in a given area is abundant only long enough for the raising of one brood (Ward 1971). Several bird species are thought to exploit an itinerant breeding strategy (Ward 1971; Walsberg 1977; Bucher 1982, 1992; Hamilton 1998). However, this behavior has been documented conclusively only in the Red-billed Quelea (*Quelea quelea*; Jaeger et al. 1986). The presence of marked queleas in distant breeding colonies within a period of a few months suggested that the birds were raising successive broods in different locations (Jaeger et al. 1986). Whether these birds were successful in either breeding attempt was not known. Phainope-

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plas (*Phainopepla nitens*) also breed in two distinct habitats during different times of the year, but whether the same birds breed in both areas has not been confirmed (Chu and Walsberg 1999). During a study of American Dippers (*Cinclus mexicanus*) in Montana's Bitterroot Mountains, I documented a case of itinerant breeding in which a banded female dipper successfully raised a brood with one male, then moved to a neighboring drainage and raised a successful second brood with a different male.

This behavior is of interest because, to my knowledge, successive monogamy (as defined by Ford 1983), or mate switching by females within a breeding season, has not been recorded in American Dippers. Dippers set up Type A (Nice 1941) linear territories of about 1–2 km in length along streams (Price and Bock 1973, Ealey 1977) and are typically thought to be monogamous within a breeding season (Kingery 1996), although several instances of polygyny have been recorded (Price and Bock 1973, Marti and Everett 1978). Dippers also generally raise second broods at the same site as or in close proximity to their first nest attempt (Sullivan 1973, Price and Bock 1983). Until now, no case of itinerant breeding has been documented in any of the five dipper species. Finally, this behavior is especially intriguing since it may have been facilitated in my study area by a human modification of the American Dipper's environment, namely, the building of bridges, which have been adopted as nest sites.

My study area was comprised of 23 streams in the Bitterroot Mountains of western Montana (Ravalli and Missoula counties: 46° 46′ N to 46° 11′ N, 114° 04′ W to 114° 23′ W). During the course of a two-year study, I surveyed streams and located and monitored 49 American Dipper nest sites (for a detailed description of study area and methods, see Osborn 1999). I banded 27 adult dippers and 33 juveniles with an aluminum USFWS band and 3 plastic color bands each. On 16 June 1997, a banded female (#8061-3405) and male (#8061-3406) successfully fledged three young from a bridge nest on Fred Burr Creek (elevation 1158 m). Less than one month later on 11 July 1997, I located female #3405 while surveying neighboring Sheafman Creek (elevation 1597 m). She and an unbanded male were feeding 3- to 5-day-old nestlings in a crevice nest between two boulders.

Based on the length of time needed to build a nest and to lay and incubate eggs, the female must have left her first territory within a day or two of her first brood's fledging. Juvenile American Dippers depend on their parents for 1–2 weeks after fledging (Sullivan 1973). One of the fledglings from the female's first brood was resighted within 1 km of its nest in August 1997, assuring that it was successfully cared for by male #3406 until its independence. Although we did not resight male #3406, the timing of the nesting chronology and the survival of at least one fledgling from the first brood indicate that female #3405 switched mates and was not just responding to the death of a first mate when she moved territories.

The female (and her unbanded mate) successfully fledged two young from her second nest. The site of this second nest was approximately 5 km southwest of her previous site in straight-line distance.

Although the distance that this female dipper moved between nesting attempts is less dramatic than those traveled by Red-billed Queleas (Jaeger et al. 1986) and Phainopeplas (Chu and Walsberg 1999), both of which may move several hundred kilometers, it is nonetheless meaningful. Dippers are altitudinal migrants, but are not known to travel extensively to exploit ephemeral food resources as are queleas (Jaeger et al. 1986) and Phainopeplas (Chu and Walsberg 1999). Price and Bock (1983) recorded movements of 22–75 km (straight-line distance) by banded dippers, but these were by dispersing juveniles over 1–2 years. Because female #3405 left her original territory, flew over several other dipper territories, switched drainages, and likely traveled more than the 5 km straight-line distance to reach her new nest site, her behavior does not represent a typical renest but rather an ecologically significant movement.

Thus far, suspected cases of itinerant breeding have all occurred in primarily granivorous or frugivorous birds (Walsberg 1977, Bucher 1982, Jaeger et al. 1986, Seutin et al. 1991, Hamilton 1998) that are faced with a seasonally abundant food supply. Although their primary prey consists of aquatic invertebrates (Mitchell 1968), itinerant-breeding dippers may be subjected to dwindling food supplies at low-elevation nest sites as the season progresses or may be exploiting a more abundant food supply at higher elevations, because the availability of aquatic invertebrates peaks later at higher elevations (Price and Bock 1983).

Because there were no natural nest sites in the lower stream reaches within my study area, bridges in these areas may have facilitated the case of itinerant breeding that I observed. American Dippers generally initiate nesting earlier at lower elevations than they do at higher ones (Sullivan 1973, Osborn 1999). In my study area, dippers began nesting significantly earlier at the lower elevation bridge nest sites than they did at the higher elevation natural nest sites (Osborn 1999). As a result, the presence of these low elevation bridge nest sites may have allowed dippers to produce an early first brood, before moving to higher elevations to produce a second brood.

Female #3405 was the only itinerant breeder that I documented. I suspect, however, that this strategy was exploited by other dippers as well. Seven of the 22 low elevation bridge-nesting pairs that I monitored in my study area fledged young before June 15, then were not sighted again on their territories. It is likely that some of these early bridge nesters moved upstream and raised second broods on natural substrates. Dippers typically exhibit a seasonal movement upstream at the end of their breeding season (Price and Bock 1983), so movements upstream after their first nesting attempt would not have been unusual.

If itinerant breeding by dippers in western Montana is not uncommon, dipper researchers should be cautioned not to underestimate the rates of second broods and productivity of individual females. Because the timing of breeding may necessitate surveying dippers at lower elevations slightly earlier in the year than those at higher elevations, double counting and therefore overestimating population estimates of breeding dippers are real risks.

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Female Blackcap Adoption of a Yellowhammer Clutch

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ABSTRACT.—Four eggs in a Yellowhammer (*Emberiza citrinella*) nest were incubated for one day by a female Yellowhammer but subsequently abandoned. The day following abandonment, the nest and the clutch were adopted by a female Blackcap (*Sylvia atricapilla*) who incubated the eggs until a single Yellowhammer nestling hatched; two eggs were depredated, and the embryo in the third egg was dead but well-developed. The young Yellowhammer was fed for 6 days until it was taken by a predator. Because there were no obvious benefits for the adopting female Blackcap, we speculate that the adoption resulted from misdirected parental behavior. *Received 7 April 2000, accepted 28 June 2000.*

In ornithological studies adoption is defined as care giving to young (Dijkstra et al. 1997) or eggs (Smith et al. 1996, Robertson 1998) by unrelated adults. Interspecific adoption has rarely been reported (but see Southern 1952, Hébert 1987, Watson et al. 1993, Lozano and Lemon 1998). In this paper, we report a case of interspecific adoption of a Yellowhammer (*Emberiza citrinella*) nest and eggs by a female Blackcap (*Sylvia atricapilla*).

The study area was a hardwood forest, approximately 85 ha, located near Dolní Bojanovice in the southeastern part of the Czech Republic (48° 52′ N, 17° 00′ E). Thirty-two species of birds breed in the forest. Blackcap and Yellowhammer were the second and third most common breeding species, with densities of 0.6 and 0.3 pairs per hectare, respectively. To test behavior of Yellowhammers toward artificial Cuckoo (*Cuculus canorus*) eggs, we placed artificial eggs into their nests after the last egg of the clutch was laid. The artificial egg resembled the Cuckoo's *Sylvia* egg type.

There are considerable differences between the nests and eggs of Yellowhammers and Blackcaps in the study area. In general, Yellowhammer nests are larger, in bushes or on the ground, and composed of different materials than those used by Blackcaps, Blackcaps nest exclusively in bushes, trees, or herbaceous vegetation. The eggs of both species are sub-elliptical and variable in color and markings. However, Yellowhammer eggs are bigger and they have a network of thin lines that are absent in Blackcap eggs. Yellowhammer nestlings hatch with smoke-gray or blackish down on head, shoulder, and back whereas Blackcap nestlings are naked. Both species primarily feed their young invertebrates (Cramp 1992, Cramp and Perrins 1994).

The Yellowhammer's nest was found at the edge of the forest on 20 May 1999. It was well-hidden, situated in a blackthorn (*Prunus spinosa*), 0.6 m above the ground. The first egg was laid 21 May and three additional eggs were laid on consecutive days. On 24 May, we added one artificial cuckoo egg to the nest. On 25 May, during the check at 16:30 (CET), the female Yellowhammer was incubating the eggs. On 26 May at 16:12, the eggs were cold and the female was not observed. During the check on 27 May at 16:36, a female Blackcap was found incubating the Yellowhammer and artificial Cuckoo eggs. On 28 May at 16:09, we removed the artificial egg to prevent abandonment of the clutch. We inspected the nest each afternoon thereafter. Two days later, two eggs disappeared. Because the nest was damaged and tipped, we presume that the eggs were depredated. However, the female Blackcap continued incubating the remaining two eggs. On 5 June, a young Yellowhammer hatched. The female Blackcap fed the young but did not continue to incubate the remaining egg. On 6 June, we removed the cold egg; the embryo was well-developed but dead. The nestling was fed by the female for 6 days and its physical development was comparable to nestlings of similar age in other Yellowhammer nests in the forest. On 11 June, the chick was taken by a predator. No male Blackcap

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was observed during our daily nest checks during incubation or during our daily (2 h each for 3 days) observations of the female feeding the nestling. Based on our observations of hundreds of Blackcap nests, normally both Blackcap parents brood and both feed the young. We did not find any other Blackcap and Yellowhammer nests within 40 or 60 m, respectively.

Explanations of intraspecific adoption (Holley 1981, Bustamante and Hiraldo 1990, Pierotti 1991, Ferrer 1993, Stutchbury and Evans Ogden 1996, Djikstra et al. 1997, Tella et al. 1997) are also applicable to interspecific adoptions. We speculate that the nest of the female Blackcap was depredated and possibly the male was killed by the predator while incubating. After the nest was destroyed, the female Blackcap may have adopted a nearby nest. Thus, the adoption we observed could be explained as a parental recognition error. The question arises: Is the Blackcap able to distinguish its own nest, eggs, and nestlings from those of other species? Moksnes and coworkers (1991) indicated that the Blackcap was known as a rejecter of Cuckoo eggs (percentage of acceptance of nonmimetic Cuckoo eggs was 23%). However, we do not know if the Blackcap shows the same recognition capability toward eggs other than Cuckoo. Noncolonial species of birds typically are unable to distinguish their own offspring from other species (Alcock 1997).

The adoption we observed was unusual and apparently rare. We did not find any similar cases in the literature. Apparent misdirected parental behavior was also reported in the adoption of Yellow Warbler (*Dendroica petechia*) nestlings by Song Sparrows (*Melospiza melodia*) in Canada (Lozano and Lemon 1998). There are no logical benefits for the adopting female to adopt the eggs and chick of an unrelated species. The Yellowhammer nestling, however, benefited from the recognition error of the Blackcap female.

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A Reassessment of the Status of Golden-winged and Blue-winged Warblers in the Hudson Highlands of Southern New York

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ABSTRACT.—Populations of Golden-winged Warblers (*Vermivora chrysoptera*) and Blue-winged Warblers (*V. pinus*) have coexisted in the Hudson Highlands for a century. Previous researchers in our study area suggested this unusual coexistence might be due to a low frequency of hybrids. However, during the 1998–1999 breeding season we found that 10% of the males were hybrids, a value similar to many studies elsewhere. We observed that hybrid males ceased singing and other conspicuous behaviors early in the breeding season. Pair formation and nesting by hybrids appeared to be rare, perhaps because of the reduced vigor of their displays. Most of the fieldwork by previous researchers in this area was conducted after the date when hybrids cease singing, which may account for prior reports of the absence of hybrids. *Received 12 April 2000, accepted 18 July 2000.*

The Golden-winged Warbler (*Vermivora chrysoptera*) has declined 7.7% annually for the last three decades in the northeastern U.S. while the Blue-winged Warbler (*V. pinus*) has declined 4.4% annually in the southern portion of its range (Sauer et al. 1999). Both species are now under Status Assessment by the U.S. Fish and Wildlife Service to determine if they should be listed under the Endangered Species Act. A decline in the abundance of early successional habitat, used by both species, may contribute to these declines (Confer and Knapp 1981). Hybridization (Confer 1992, Gill et al. in press) may be the major cause of the Golden-winged Warbler decline (Canterbury et al. 1993, Gill 1997, Confer and Larkin 1998).

In the Hudson Highlands, extending from northeastern New Jersey through southern New York and into Connecticut, the two species have coexisted for nearly a century (Eaton 1914, Frech and Confer 1987, Scully 1997). Three studies revealed that hybrids were rare in this region (Frech and Confer 1987, Scully 1997, and Confer et al. 1998). These studies raised the exciting possibility of a localized, species-isolating mechanism that could account for the survival of these sympatric populations.

In 1998–1999, we studied nesting by Golden-winged and Blue-winged warblers throughout Sterling Forest State Park, New York. The park encompasses most of the sites studied by Frech and Confer (1987), all of the area surveyed by Confer and coworkers (1998), and is contiguous to the area surveyed by Scully (1997). The objective of our study was to determine whether the two species continue to coexist and to evaluate the frequency of hybrids in the community.

STUDY AREA AND METHODS

We made observations in the Hudson Highlands, primarily within Sterling Forest State Park, NY (41° 11′ N, 74° 14′ W). We censused all sites with known concentrations of *Vermivora*, as indicated by data from the Palisades Interstate Park Commission and personal observations of local birders (J. Gebhards, J. Yrizarry). Habitats consisted of meadows, power-line rights-of-way, and wetlands. Field observations of Golden-winged and Blue-winged warblers and their hybrids were compiled by Confer and three assistants in 1998 and 1999. In 1998, we made observations six days a week from 11–25 May and 10–16 June and from 27 June to 1 July. In 1999 observations were made six days a week from 11 May to 5 June and from 28 June to 2 July. Observations began about 05:15 EST and continued until at least 13:00.

We monitored all males that were accessible throughout the breeding season. We spent approximately 10 person-hours in the territory of each male of pure phenotype to determine territorial boundaries and nesting success. We often used a taped playback with Type I and Type II songs (following Gill and Lanyon 1964) of both Golden-winged and Blue-winged warblers to determine if males were present in a previously uncensused study area. We also used taped playbacks to lure birds to mist nets and color-banded birds in areas with a high breeding density.

Roadside surveys of *Vermivora* were conducted in Sterling Forest State Park 25 May 1997 (Confer et al. 1998) and 9 June 1999. Both surveys utilized a tape of Golden-winged and Blue-winged warblers Type I and

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TABLE 1. Golden-winged and Blue-winged warblers and their hybrids observed during surveys in the Hudson Highlands from 1986–1999.

Reference	Dates	Number GW[a]	Number BW[b]	Number BR[c]	No. introgressed[d]
Scully, 1997	10 May–15 July 1986	17	16	0	1 ~[e] BW
Scully, 1997	13 May–27 June 1987	15	13	0	1 ~ GW
Scully, 1997	8 May–26 June 1988	23	34	0	1 ~ BW
Frech and Confer, 1987	30 May–28 June 1986	7	13	0	0
Confer et al. 1998	25 May 1997	18	12	0	1 ~ BW
This study	11–25 May 1998	19	14	5	0
This study	11 May–26 May 1999	43	29	8	1 ~ BR
This study	9 June 1999	4	13	0	0
Total individuals	1998+1999	62	43	13	

[a] Golden-winged Warbler.
[b] Blue-winged Warbler.
[c] Brewster's Warbler.
[d] Introgressed birds resemble parental phenotype yet have some hybrid characteristics.
[e] Indicates species most resembled.

Type II songs played throughout a 3-min count period. The same 32 roadside sites were used both years.

RESULTS

During 1998 and 1999, we observed a total of 13 Brewster's Warbler hybrids (Table 1). Two hybrid males were observed only briefly. The other 11 Brewster's Warblers initially displayed typical territorial behavior by singing frequently from conspicuous perches in treetops that surrounded a semi-circular area. These 11 hybrid males comprised 10% of the total territorial *Vermivora* males.

In 1998, we detected 5 territorial male Brewster's Warblers including 1 Brewster's × Brewster's Warbler pair that successfully fledged young. The frequency and duration of singing by this successful hybrid male did not qualitatively differ from singing by males of pure phenotype. However, 3 of the 4 remaining male Brewster's Warblers could not be relocated after 10 June, and the fourth after 27 June.

In 1999 we spent about 15 person-hours at each of the six locations where a hybrid had shown territoriality earlier in the season. We arrived at each location before 06:00 at least once during late May and early June when males of pure phenotypes were singing. One Brewster's Warbler sang in an area between two singing Golden-winged Warbler males on 13 and 14 May. We discovered both Golden-winged Warbler nests after searching the entire area during several mornings. Despite our effort, we did not see any Brewster's Warblers in this area after 14 May until 24 June when a silent, male Brewster's Warbler was observed foraging. Another Brewster's Warbler was seen adjacent to our most intensively studied area. From 12–26 May, it responded strongly to a taped playback, but was not detected after 26 May despite several, prolonged uses of taped playbacks. In sum, in 1999 two of six hybrid males quit singing or exhibiting other conspicuous behavior before 15–16 May and the remaining four quit before 24–26 May. Males of both parented phenotypes continued to sing long after Brewster's males could not be located.

We used a similar tape at the same 32 roadside survey sites in 1997 and 1999. However, the 1999 census was conducted on 9 June, 15 days later than in 1997. No hybrids were detected in either survey (Table 1) although three stops were at locations where Brewster's Warblers were detected earlier in 1999. In comparison, the numbers of Blue-winged Warblers detected was almost identical in the two years; the number of Golden-winged Warblers declined from 18 to 4, but this might not mean that Golden-winged Warblers were declining. In 1999 we failed to get a Golden-winged Warbler response at four stops that were near active Golden-winged Warbler nests. The decline in number of Golden-winged Warblers is probably due to the census being made 15 days later in the season.

We detected very little evidence of nesting Brewster's Warblers during this study. In 1998 we located the nest of a Brewster's × Brewster's pair. We saw a Brewster's Warbler male courting a female only one other time and never saw any fledglings associated with any Brewster's Warbler other than the hybrid pairing. In contrast, we found nests for about 50% of the males of the parental phenotypes and noted fledglings for an additional 10%. Although we spent more time looking for the nests of the parental phenotypes than hybrids, we spent enough time in the area where Brewster's Warblers had been seen that we should have found their nests or observed courtship or fledglings. Although successful nesting by hybrids that obtain mates is documented (e.g., Confer 1992; Gill et al. in press), the proportion of hybrid males that obtain mates seems to be quite low in the Hudson Highlands.

DISCUSSION

During two years of intensive observations, 12 of 13 Brewster's Warbler males stopped all singing by 24–26 May. Birds of both parental phenotypes frequently sang up to two weeks after the hybrid song stopped. This temporal sequence could account for the misleading absence of hybrids in previous studies in this area. Frech and Confer (1987) began their observations on 30 May and Confer and coworkers (1998) conducted their census on 25 May. Both studies were probably too late to detect any Brewster's Warblers. Scully (1997) conducted a 3-yr study of *Vermivora* in New Jersey contiguous to Sterling Forest State Park. He detected about 90 territorial males. Three birds had some indication of hybrid plumage but none had the typical hybrid Brewster's or Lawrence's warbler plumage. Scully began his observations as birds arrived in the spring; consequently, he was in the field when Brewster's Warblers would be singing. However, his observations were limited primarily to weekends (Scully 1997). Consequently, he could not have spent much time in the field during the 1–2 weeks while Brewster's Warblers sang. It is possible that the limited observations early in the season account for the absence of hybrids in Scully's observations.

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Singing by Female Chestnut-sided Warblers

Bruce E. Byers[1, 4] and David I. King[2, 3]

ABSTRACT.—We recorded examples of complex, highly variable, song-like vocalizations uttered by female Chestnut-sided Warblers (*Dendroica pensylvanica*) in Massachusetts and New Hampshire. These songs occurred only during a brief period just after females arrived on the breeding grounds and were almost invariably associated with intense social interactions. Although the timing and context of the songs might suggest a territorial defense or other communicative function, the songs bore no resemblance to male songs, were uttered infrequently, and were used by only a small proportion of females. Therefore, we believe it is unlikely that the songs could be reliably recognized and interpreted by conspecifics. Perhaps the vocalizations are byproducts of seasonally high levels of circulating sex hormones, as suggested by the prolonged singing that we observed in a captive-reared female that had been implanted with testosterone. *Received 24 April 2000, acccepted 17 July 2000.*

The most conspicuous feature of vocal communication in songbird species that breed in North Temperate latitudes is loud, often elaborate singing by males. Compared to these male songs, the vocalizations of Temperate Zone female songbirds are generally much less noticeable, consisting mainly of structurally simple chips and call notes. Nonetheless, female vocalizations may also include complex songs (Langmore 1998). Such female singing has been documented in few temperate songbird species, but this scarcity may be due more to the nature of female singing than to its actual prevalence.

Unlike their tropical counterparts, many of whom utter songs whose profusion and acoustic structure are comparable to those of males (Morton 1996), Temperate Zone female singers, with some notable exceptions [e.g., Northern Cardinal (*Cardinalis cardinalis*); Halkin 1997] tend to sing in a manner distinct from that of males. In particular, females may sing only infrequently or only during a brief time period [e.g., Chiffchaff (*Psylloscopus collybita*); King 1992], or may produce songs that sound different from those of males [e.g., Red-winged Blackbird (*Agelaius phoeniceus*); Beletsky 1983]. In addition, singing may be limited to a few females in a population [e.g., Prairie Warbler (*Dendroica discolor*); Nolan 1978]. Thus, the acoustically distinct, infrequently heard songs of females may go unnoticed by human observers amidst the cacophony of male song.

The ease with which female singing can be overlooked became evident to us when we first became aware that female Chestnut-sided Warblers (*Dendroica pensylvanica*) sing. Each of us had separately studied Chestnut-sided Warblers for several years before noticing that females occasionally utter vocalizations that are much longer and more complex than the more common call notes of the species. Once we noticed these female songs, however, we focused more attention on seeking them out and were able to record many instances in which females sang. Here we report on the behavioral contexts in which those songs occurred and discuss whether the songs have functional significance.

METHODS

Over the course of various investigations of the breeding biology (D.I.K.) and male songs (B.E.B.) of Chestnut-sided Warblers, we made tape recordings of female songs whenever we encountered a singing female. Chestnut-sided Warblers are sexually dimorphic, and the sex of most individuals is readily determined in the field; occasional individuals with ambiguous plumage characteristics can be sexed by behavioral cues. The duration of recorded song samples ranged from 3–30 min. We sampled the songs of about 26 females (this number is an estimate as only about half of the recorded females were color-banded; whenever we made multiple recordings of female song on the

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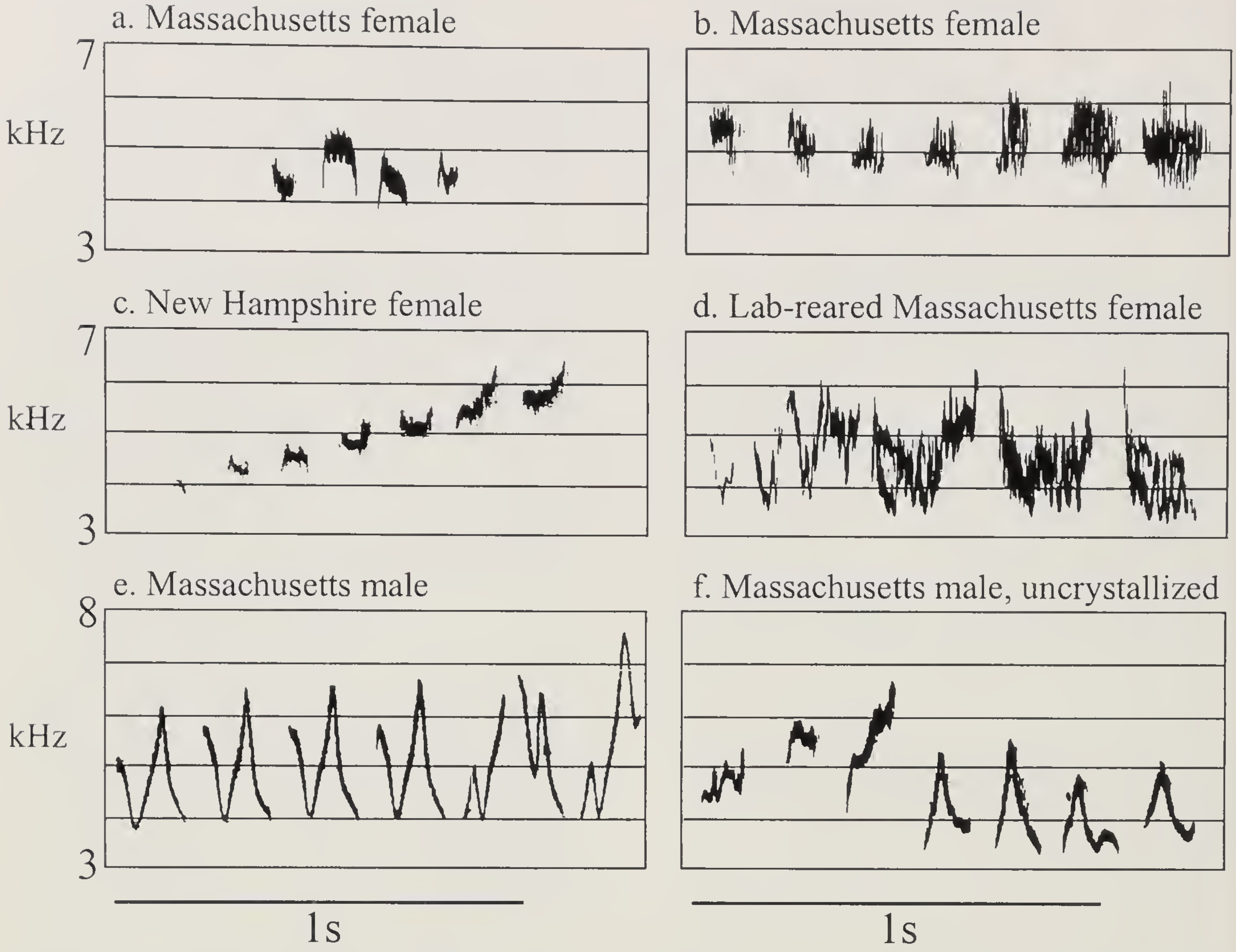

FIG. 1. Sonagrams of songs from six different Chestnut-sided Warblers, showing that female songs (a–d) bear little resemblance to either normal (e) or uncrystallized (f) male songs. Songs a, b, c, and e were recorded in the field; songs d and f are from hand-reared birds.

territory of a particular color-banded male, we assumed that each sample was of the same female). We recorded during May of 1988–1990, 1995, 1997, and 1999 at two locations, one in western Massachusetts and one in New Hampshire (1997 only). The Massachusetts site was in Savoy State Forest, Berkshire County (42° 40′ N, 73° 3′ W); the New Hampshire site was in White Mountain National Forest, Coos County (44° 12′ N, 71° 32′ W). Songs were recorded on cassette tapes using Sony TCM-5000, Sony TCD5 Pro II, and Marantz PMD recorders, with either a Sennheiser ME62 microphone mounted on a 58 cm parabolic reflector or a Sennheiser ME88 microphone.

In addition to the field recordings, we also recorded the songs of a female Chestnut-sided Warbler that had been hand-reared in the laboratory. This female was collected at six days of age and housed in a soundproof room with 18 other male and female conspecifics. Sixteen of these conspecifics were hand-reared individuals of the focal female's age cohort; the other two were wild-caught adult males. The adult males sang consistently during the six weeks immediately after the focal female was introduced to the room and again the following spring, when the eight hand-reared males also began to sing. At the onset of male singing during the second spring, we implanted the focal female with a 1 cm length of silastic tubing (1.5 mm inside diameter) containing testosterone. After implantation, the female began singing and was subsequently moved to an acoustically isolated chamber, where her vocalizations were recorded for two hours per day for 14 days.

RESULTS

We made field recordings of 469 songs in 40 samples from approximately 26 female Chestnut-sided Warblers. Four samples from two individuals were from New Hampshire; the remaining samples were from Massachusetts. The 26 singing females we encountered represented fewer than 5% of the total number of females present on territories on which we spent five or more hours observing.

Female songs (Fig. 1A–D) had a buzzy quality that sounded quite different from the clear, warbled notes of male songs (Fig. 1E).

Some female songs (e.g., Fig. 1C) were reminiscent of those of male Prairie Warblers. Although all recorded songs had the same general structure (a series of 4–8 elements, each of 60–130 msec duration), songs were variable among females, with no two birds singing matching songs. This lack of stereotypy extended to the singing of individual birds; rarely did a bout of singing contain two identical songs. The inconsistency among songs within a bout was reminiscent of uncrystallized singing by male Chestnut-sided Warblers (though the songs themselves did not resemble uncrystallized male songs, Fig. 1F).

All song samples were recorded within a narrow range of dates (15–23 May in Massachusetts and 29–31 May in New Hampshire, where Chestnut-sided Warblers arrive on the breeding grounds about a week later than in Massachusetts). We heard no female songs outside of this range of dates, which corresponds to the warblers' period of courtship and pair-formation. In all cases in which a female's arrival date was known (10 birds), songs were recorded only on the first, second, and/or third days following arrival. All singing females for which we observed nest construction (19 birds) uttered songs only before construction began.

Most female songs occurred during or after a social interaction involving the female, her mate, or both. The early courtship period in which all female singing occurred is also a period of intense male-male aggression, and most female singing took place near the scene of a chase or fight between the singing female's mate and another male. Thirty-five of our 40 samples of female singing included at least one male-male fight or chase, and in only one sample was the singing female situated more than 5 m from the interacting males. The singing female's proximity to interacting males also meant that most female singing took place in the vicinity of territorial borders. In several instances (seven samples), other non-singing females were also present nearby, and the relatively secretive habits of female Chestnut-sided Warblers mean that unnoticed non-singing females were probably near singers in additional cases. In three samples, singing females were chased by their mates.

Our lab-reared, testosterone-implanted female sang almost continuously during her 14 sampling periods at a rate of about 4 songs per minute. Thus, her singing was far more extensive than that of any wild female that we encountered. Her songs (Fig. 1d) were structurally similar to those of wild females but did not match any field-recorded songs. None of 21 other unimplanted female Chestnut-sided Warblers that we hand-reared concurrently with the focal female uttered any song.

DISCUSSION

The rarity of female Chestnut-sided Warbler singing raises the question of whether such an infrequently used signal can serve a communicative function. Although rarely used, female songs have been shown to have a communicative function in several species (reviewed by Langmore 1998), females of those species use songs that are similar in structure to male songs and that are used (even if infrequently) by all or most females in a population [e.g. Song Sparrow (*Melospiza melodia*), Arcese et al. 1988; White-crowned Sparrow (*Zonotrichia leucophrys*), Baptista et al. 1993; and Alpine Accentor (*Prunella collaris*), Langmore et al. 1996]. In these species, females use signals of a class that is likely to have been previously encountered by conspecific individuals and that might reasonably be expected to play a role in the species' communicative lexicon.

In contrast, singing by female Chestnut-sided Warblers consists of sporadic use of idiosyncratic songs by very few individuals, a pattern that is shared by other temperate-breeding wood warblers, including Prairie Warblers (Nolan 1978), Wilson's Warblers (*Wilsonia pusilla,* Gilbert and Carroll 1999), Northern Parulas (*Parula americana,* Jones 1966), and Yellow Warblers (*Dendroica petechia,* Hobson and Sealy 1990). Although we find it difficult to imagine circumstances in which potential receivers would evolve or learn a response to a signal that is used by only a few individuals in a population and rarely even by them, some researchers have proposed that female singing in wood warblers is functional. For example, Hobson and Sealy (1990) suggested that female songs of Yellow Warblers serve as a signal of intrasexual aggression. These authors based their conclusion on their observation that the rarely heard songs of female Yellow Warblers always occurred in the context of equally rare female-female aggression, and on the investigators' ability to occasionally induce female singing by presenting a model of a female Yellow Warbler. Similarly, Gilbert and Carroll (1999) inferred function from the context in which they observed singing by a female Wilson's Warbler. Because the female sang on her first day in residence on a male's territory, sang in close proximity to the male, and interspersed her songs with chip notes (as if using the songs to replace some of the chips in a sequence), the authors speculated that female song might serve to facilitate pair formation.

In our study, we were not able to infer function from the context in which female Chestnut-sided Warbler songs occurred, even though the general context of songs was consistent. Female songs invariably occurred during courtship and mostly close to a male, which might suggest a courtship function. But the songs also occurred largely near territorial borders while those borders were being actively defended by males, which might suggest a territorial defense function (although singing was not associated with overt female-female aggression, which we observed on a few occasions but never accompanied by female singing). In fact, the period in which female singing occurred coincided with so much intense social activity (males establishing or attempting to expand territories, females prospecting for breeding sites, males courting and guarding females, disruptions caused by new arrivals of both sexes) that it was often difficult for an observer to ascertain the precise nature of any particular interaction that was associated with a female song.

Our observations of female singing can neither establish nor rule out the functional significance of the songs, but they are consistent with the explanation that the songs are functionless responses to highly stimulating social situations. The songs occur at a time in the breeding cycle at which levels of circulating sex hormones in Temperate Zone, migratory songbirds reach their peak (Wingfield and Farner 1978), and in social contexts that can be extremely stimulating or stressful. Some females, perhaps those with comparatively high initial circulating hormone levels, might be pushed past some hormonal threshold by an especially potent social stimulus. In these cases, the female bird's latent song production apparatus might be briefly stimulated, a transient condition that we induced on a more permanent basis in our hormone implanted female in the laboratory.

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Black-vented Oriole Nests Inside a Cabin in El Salvador

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ABSTRACT.—A pair of Black-vented Orioles (*Icterus wagleri*) successfully fledged young from a nest inside a log cabin in the Montecristo National Park, El Salvador. This is the first breeding record of the species for El Salvador. The nest was hammock-shaped, 18 × 20 cm outside, 6 cm deep inside, and contained four eggs. After the first clutch failed, the pair renested using the same nest, incubating and rearing three young over 34 days. *Received 1 Feb. 2000, accepted 11 July 2000.*

Orioles (*Icterus* spp.) usually build hanging nests attached by woven grasses and other plant fibers to twigs near the ends of tree branches or to other kinds of plant material, such as shrubs, reeds, large leaves, and Spanish moss (Baicich and Harrison 1997, Jaramillo and Burke 1999). Several tropical species typically attach their nests to the undersides of large palm leaves or banana fronds (Jaramillo and Burke 1999). Álvarez del Toro (1971) described the nest of the Black-vented Oriole (*Icterus wagleri*) as hanging like a hammock under a palm or banana leaf, with the fibers woven into the leaf material. The nesting habits of the Black-vented Oriole are otherwise poorly known. Timing of nesting can be surmised as June and July based on the collecting of birds in breeding condition in Oaxaca (Binford 1989). A single clutch contained three eggs in Guatemala (Salvin 1859).

The use of artificial substrates to attach nests is unusual in orioles, with notable exceptions being the frequent use of telegraph or electric wires by Altamira Orioles (*I. gularis*), Streak-backed Orioles (*I. pustulatus*), and Yellow-tailed Orioles (*I. mesomelas*; Jaramillo and Burke 1999). The only oriole reported to attach its nest to man-made structures other than power lines is the Hooded Oriole (*I. cucullatus*), which has been reported using the eaves of houses (Bent 1958).

On 15 June 1999, we found a pair of Black-vented Orioles nesting inside a log cabin at Montecristo National Park, El Salvador (14° 23′ N, 89° 22′ W, 1900 m elevation), overlooking an area known as Los Planes de Montecristo. The cabin was in a large flower garden about 20 m from an old grove of Mexican cypress (*Cupressus lusitanicus*). It was surrounded by a chain-link and barb-wire fence, some bushes and a small tree, which provided perches for the orioles as they approached and exited the cabin. The orioles entered and exited through wide cracks between the walls and the roof or through the front door when it was left ajar. Glass in the front door and several windows permitted natural sunlight to illuminate the cabin interior.

The day we found the nest, the single nestling flopped out of the nest, perhaps because we startled it or because of the adults' agitated warning calls. The bird could barely fly. Because we thought the adults were likely to abandon the nest with our presence, we helped the bird out of the cabin and discovered that the adults had disappeared. The young bird fluttered into the garden and we never saw it again. No other young or eggs were in the nest.

The adults were again in the cabin on 21 June and on the evening of 22 June at least one entered the cabin late at night (around 23:00 CST). They evidently had abandoned the first young and began to renest, using the same nest. Four eggs were laid 23–26 June. One egg measured 25.9 mm × 16.4 mm. It was oval, cream colored, with dark brown and yellowish blotches so dense at the broad end that they merged into one large irregular blotch. Almost no blotches were at the tapered end.

We left the cabin on 27 June (having lived

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FIG. 1. Nest of the Black-vented Oriole in El Salvador.

in it for 12 days) and returned 19 July. The new brood had hatched and grown large. By 28 July we could discern at least three nestlings. On 30 July, A. L. Rosales de Komar saw two of the three nestlings leave the nest and fly after the adults between 10:00 and 11:00. The third young left during the same time, but unseen. The birds went out the front door, which had been left ajar. After the young fledged, we removed and photographed the nest with the fourth egg still intact (Fig. 1). [Voucher photographs of the nest, adult, and fledgling have been deposited at the Academy of Natural Sciences, Philadelphia, Pennsylvania (VIREO #v06/35/001–004).]

Thus, incubation and rearing of young was completed in 34 days. If the nestling from the first clutch abandoned the nest four days prematurely (it was able to fly a short distance), the estimated laying date of its egg would be 15 May. Nest building would have begun several days earlier.

The nest hung by two attachments from a plastic-coated electrical wire attached to a wooden crossbeam of the ceiling, adjacent to a florescent light, and under a green corrugated galvanized iron ceiling. The nest hung 2.7 m above the cabin floor and about the same distance from the front door. The nest was hammock shaped, with the two attachment points 18 cm apart. The attachment points were 4 cm below the ceiling. The nest height was 20 cm. The cup of the nest was 13 cm below the attachment points and 6 cm deep. The nest was not symmetrical; fibers on one side were strung between the two attachment points 5.5 cm above the nest cup (about 7.5 cm below the attachment points). The outside of the nest included ten white chicken (*Gallus gallus*) feathers. Several more such feathers littered the floor beneath. Other materials of the outer nest surface included rigid black hairs (one was 6.3 cm long) that may have been horse hair, fern roots and/or hyphae of fungi, and fine dried grass fibers (one 9 cm long). Inside was a loose cup, woven of fine grass fibers (one was 6.7 cm long), mixed with contour feathers from chickens.

The adults arrived together to feed the young. Although both birds always had food in their beaks, only one would go to the nest, frequently feeding the young with green conehead katydids (*Neoconocephalus* sp., Tettigoniidae). The other adult waited outside the cabin, usually giving loud calls, and left with the first bird, without delivering the food it carried. The second bird once swallowed the food after flying to a nearby cypress tree; it then gleaned for insects among the foliage and found a brown caterpillar that it also swallowed.

On the afternoon before fledging (29 July), the nestlings were almost constantly calling. One crawled outside the nest but immediately went back in. An adult, the presumed female, visited more frequently than on previous afternoons (we were not present during the mornings). Between 17:20 and 18:13, this adult fed young 12 times, on average once every 4.4 minutes. At 17:39 the other adult went to the nest but did not feed the young. It repeated this action at 17:47, vocalizing (a nasal grunt) twice next to the nest. At 18:20 it visited again, vocalizing approximately 10 times, seemingly very excited. This same vocalization was given almost constantly by the adults when they were outside the cabin. At 18:27, one of the adults visited the nest and vocalized twice; it was almost dark and we could not tell if the bird fed the young. We interpret these last few visits before fledging, which were different from previous nest visits because the adult vocalized and did not feed young, as an attempt to encourage the young to leave the nest.

The Black-vented Oriole was not previously reported breeding in El Salvador (Komar 1998). It was thought to be a non-breeding visitor of the dry season (Thurber et al. 1987). All published records from El Salvador are from October through February (Dickey and van Rossem 1938, Steinbacher 1958) while our observations of a nesting pair were made in June and July. O.K. also observed one adult Black-vented Oriole at Los Planes de Montecristo on 12 August 1995. Possibly the same pair built another nest inside the same cabin in 2000, with eggs present 15 July (J. Porras, pers. comm.).

Why did the orioles select the interior of a building as a nest site? There are several possible advantages. The added concealment of the nest might reduce exposure to some predators, such as snakes, mammals, and birds (Collias and Collias 1984). The artificial habitat might reduce the presence of insects such as botflies (*Philornis* sp.), mosquitoes, or other nest parasites. The cabin provided extra protection from the wind, rain, and sun, but the natural nest substrate of a large palm leaf or banana leaf would provide similar protection. Another possibility is that appropriate nest substrates in the area were scarce or unavailable. No palm trees were present within several kilometers, but we observed several banana plants near a homestead.

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First Record of Brown-headed Cowbird Egg in a Lesser Scaup Nest

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ABSTRACT.—On 16 June 1999, I found a Lesser Scaup (*Aythya affinis*) nest parasitized by a Brown-headed Cowbird (*Molothrus ater*). On 22 June the female scaup had begun incubating the 10 scaup eggs but the cowbird egg was missing, presumably ejected by the female scaup. *Received 27 March 2000, accepted 3 July 2000.*

On 16 June 1999, while searching for waterfowl nests near Erickson, Manitoba (50° 30′ N, 99° 55′ W) I found a Lesser Scaup (*Aythya affinis*) nest containing a Brown-headed Cowbird (*Molothrus ater*) egg and six Lesser Scaup eggs. This is the first published record of a Lesser Scaup nest containing a Brown-headed Cowbird egg (see reviews by Friedmann and Kiff 1985, Johnsgard 1997). I calculated the clutch initiation date to be 11 June based on candling of the six fresh scaup eggs in the nest at the time of discovery. On 22 June I checked the status of the nest and used a field candler to determine that the female scaup had begun incubation (Weller 1956). The nest contained 10 scaup eggs but the cowbird egg was missing. I looked around the nest for the cowbird egg but did not see it in the vicinity. It is likely that the relatively large size of the scaup's bill enabled it to grasp and eject the cowbird egg from the nest (Clayton and Moore 1997). On 26 June I found that the nest had been depredated. I do not know whether the parasitism event affected the eventual fate of the scaup nest, but avian predators might use cowbirds as a cue to find nests.

On the expected day of hatching (16 July), I recorded microhabitat and spatial location variables of the nest. The nest was located overwater in sedge (*Carex* spp.) vegetation. The vegetation near the nest was 0.7 m tall, formed a 35% canopy cover, and had a Visual Obstruction Reading of 6.6 (Robel et al. 1970). The nest was located in 0.1 m of water, 3 m from open water, 3 m from the nearest edge, and 7 m from the edge of the wetland.

While many warblers, vireos, phoebes, and sparrows are acceptor species of cowbird eggs, waterfowl are rejecters (Friedmann and Kiff 1985, Johnsgard 1997). Brown-headed Cowbirds have been documented as successfully parasitizing 144 of 220 species' nests in which their eggs have been observed (Friedmann and Kiff 1985, Johnsgard 1997). Lesser Scaup can now be added to the current list of 76 rejecter species to Brown-headed Cowbird parasitism. The Blue-winged Teal (*Anas discors*) is the only other anseriform documented to be a rejecter of Brown-headed Cowbird parasitism (Friedmann and Kiff 1985).

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Diet and Foraging Behavior of Nesting Roadside Hawks in Petén, Guatemala

Theresa Panasci[1,2,4] and David Whitacre[3]

ABSTRACT.—In 1993 and 1994, we collected data on the diet and foraging behavior of Roadside Hawks (*Buteo magnirostris*) in primary tropical forest with slash-and-burn farming landscape nearby. We identified 140 prey items brought to nests: 90 in the farming landscape and 50 in the forest. Reptiles (57.1%, mostly lizards) and amphibians (24.3%) were the main prey types delivered to nestlings in both habitats, but size and type of prey differed between nests in the two habitats. Relatively more amphibians and reptiles were delivered to slash-and-burn nests and more mammals and insects to forest nests. In 40 of 44 prey capture attempts, Roadside Hawks utilized the typical *Buteo* technique, searching for prey from a perch and attacking once prey was sighted. In addition, two aerial attacks were directed at a flying and at a perched bird, and hawks walking on the ground twice captured beetles. Of 44 capture attempts, 84% were successful. In the forest, half of 32 attacks were launched from perches protruding above vegetation along a road or in clearings; the other half were launched from perches beneath the forest canopy. These hawks often took advantage of special hunting opportunities: attending army-ant swarms, taking many frogs immediately after rain showers, and catching prey fleeing from fires. *Received 14 Feb. 2000, accepted 20 June 2000.*

The diet and hunting habits of most tropical raptors are not fully documented. The Roadside Hawk (*Buteo magnirostris*) is a dietary generalist and most published accounts relate a varied diet consisting of amphibians, reptiles, insects, and mammals. Early collectors reported that Roadside Hawk stomach contents contained a variety of organisms including lizards, salamanders, small snakes, caterpillars, spiders, grasshoppers, beetles, mice, and birds (Dickey and van Rossem 1938, Lowery and Dalquest 1951, Tashian 1953, Haverschmidt 1962). The few quantitative studies of the diet and hunting behavior of the Roadside Hawk were based on small samples. As part of a broader study on the comparative ecology of Roadside Hawks in primary forest and in slash-and-burn farming habitats, we collected data on prey brought to eight nests in these two habitats and on foraging behavior.

METHODS

Our two study areas were 25 km apart and located in and adjacent to Tikal National Park (17° 11′ N, 89° 48′ W), Guatemala. The 576 km^2 park supports mid-height to tall sub-perennial tropical forest (Pennington and Sarukhan 1968) that is mostly unlogged, primary forest. Forest vegetation varies as a continuum along a topographic and soil-type gradient from well drained to poorly drained (Schulze and Whitacre 1999). Topography is gently rolling, mostly 200–350 m in elevation. Mean annual precipitation is 1350 mm with a pronounced dry season from February to May. There are no permanent streams in the area; during the dry season, surface water is found in scattered water holes. Slash-and-burn farming was 10 km south of the park within the buffer zone of the Maya Biosphere Reserve. This habitat mosaic contained disturbed fragments of primary forest, crop fields [mostly corn (*Zea mays*)], pastures, clear-cuts, bracken fern (*Pteridium aquilinum*) monocultures, and extensive areas in various stages of succession from low brush to 10 m second-growth. Less than 10% of the study area was covered by mature forest remnants.

During 1994, T.P. and three field assistants studied Roadside Hawk food habits at eight nests in the two study areas. We made observations from blinds on the ground and platforms in trees at least 30 m from nest trees using 10× binoculars and spotting scopes. Nests were observed from dawn to dusk (13 h) to monitor birds during all daylight hours, with a change of observers at mid-day. We recorded prey type and size at five slash-and-burn nest sites observed for 243 hours and at three forest nest sites observed for 151 hours, April–June 1994. We identified prey items as precisely as possible, often to genus, estimated their length, and placed them in the following size classes: tiny (≤ 5 cm: insects and the smallest lizards), small (6–25 cm: most lizards and frogs), and medium (> 25 cm: mostly

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mammals and snakes). We used G-tests to compare prey types and sizes in the diet in the two habitats.

In 1993 and 1994, we collected data on foraging behavior during nest observations, nest searches, and monitoring nesting pairs. We also observed foraging bouts whenever we observed a Roadside Hawk attacking prey. For each foraging attempt we recorded the date, time, habitat (edge, continuous forest, farming landscape), hunting technique, perch height, prey location, and success or failure of the attack. All statistical tests were performed using the SAS System version 6 (SAS Institute, Inc. 1989). Mean values are presented with standard deviations.

RESULTS AND DISCUSSION

Hunting behavior.—Roadside Hawks used still-hunting (hunting from a perch and dropping down to capture a prey item) 40 of 44 foraging attempts (91%) and ground-hunting (walking on the ground and seizing prey in the talons) twice (4.5%). The hawks made two aerial attacks on birds (4.5%). Thirty-seven of the 44 foraging attempts (84%) were successful. Both ground-hunting attempts were successful, yielding beetles (Coleoptera), and one of the two aerial attempts was successful, yielding a Black-cowled Oriole (*Icterus prosthemelas*). Of the 40 still-hunting attempts, 34 were successful (85%). We could not compare success in the two habitats because only eight foraging attempts were observed in the farming landscape.

The mean height of the perch from which still-hunting attacks were launched was 6.4 ± 4.5 m (range = 1–17 m). The mean perch height of the eight still-hunting attempts in the slash-and-burn landscape was 8.9 ± 4.3 m and all attacks originated from perches taller than the surrounding vegetation. In the primary forest, half of the observed attacks (16 of 32) were launched from perches (trees) protruding above areas of lower forest canopy, either along a dirt road (n = 11) or an artificial clearing (n = 5). Four Roadside Hawks launched hunts from perches about 5 m high along forest edges and successfully captured adult cicadas on tree trunks or other vegetation 1–2.5 m above the ground. We watched one banded male descend from a 2.5 m high perch along a clearing edge, capture a tarantula at the opening of its burrow, remove the spider's legs, and consume it there.

Sixteen of the 32 still-hunting hawks hunted from perches beneath the forest canopy. On 13 occasions these hawks hunted from perches 1–15 m from the ground where they hunted insects (n = 7) fleeing from army ant swarms (including *Eciton* spp.) and lizards (n = 6) on the ground or in vegetation requiring a shallow angle of descent. In the other three, Roadside Hawks dropped steeply from tree limbs averaging 14.8 ± 2.3 m above ground and seized lizards or cicadas from the perch tree bole (n = 2) or neighboring tree bole (n = 1) about 5 m below their perch.

TABLE 1. Prey delivered to nests by Roadside Hawks in the two study areas in Petén, Guatemala in 1994.

Prey type	Primary forest	Slash-and-burn
Reptiles	23	57
Sceloporus spp.	0	4
Anolis spp.	9	0
Corythophanes spp.	0	1
Unidentified lizards	11	51
Skinks	2	0
Snakes	1	1
Amphibians	9	25
Frog	9	24
Toad	0	1
Mammals	9	2
Heteromys spp.	4	0
Ototylomys spp.	0	2
Unidentified rats	2	0
Sciurus deppei	1	0
Bats	2	0
Birds	0	2
Insects	9	4
Cicadas	7	1
Grasshoppers	2	2
Caterpillars	0	1
Total	50	90

Dickey and van Rossem (1938) observed a Roadside Hawk snatch a Blue Honeycreeper (*Cyanerpes cyaneus*) from a feeding flock. We observed an unsuccessful aerial pursuit of a Squirrel Cuckoo (*Piaya cayana*) through low secondary vegetation about 1–2 m in height (Panasci 1995). The other aerial attack by a Roadside Hawk was the successful capture of a Black-cowled Oriole (Panasci 1995).

Diet.—We identified 140 prey items, 90 at slash-and-burn nests and 50 at forest nests (Table 1). Reptiles comprised 57.1% of the nestling diet overall and 46% of prey at forest nests and 63.3% of the prey at the slash-and-burn nests. Amphibians were the second most frequent prey, making up 24.3% of nestling diets overall. Insects (especially cicadas and grasshoppers) comprised 9.3% of prey items, mammals 7.9% (with 1 squirrel, 8 other rodents, and 2 bats), and birds 1.4%. Reptiles and amphibians comprised 81.4% of the prey delivered to all nests. Lizards, frogs, and insects typically were delivered to nests intact, but most mammals were decapitated or partially eaten before delivery. Birds were plucked before they were brought to the prey exchange site. Prey types delivered to nests differed significantly with habitat (G-test: $G = 15.11$, 3 df, $P = 0.002$), as did prey size (G-test: $G = 19.10$, 2 df, $P = 0.001$). Relatively more mammals and insects were delivered to forest nests, and more amphibians and reptiles to slash-and-burn nests (Table 1).

In the slash-and-burn habitat, 4 of 90 prey items were classified as tiny, 81 as small, and five as medium. In the forest plot, prey items did not fall predominantly in one size category and were distributed as follows: 11 tiny, 29 small, and 10 medium. Most prey items were in the small size category because it included most of the lizards. Lizards ($n = 78$), made up 55% of the prey items delivered to nests in both habitats (Table 1). *Anolis* lizards, which are mainly arboreal and occur in the forest interior, were identified only at nests in the primary forest, whereas *Sceloporus* lizards (mainly terrestrial and found in open habitats) were identified only at nests in the farming landscape. We did not estimate prey biomass, but doing so would probably reduce the importance of insects and increase the importance of mammals.

Various authors have characterized Roadside Hawks as opportunistic hunters (Dickey and Van Rossem 1938, Robinson 1994). We observed these hawks to opportunistically exploit prey types during brief periods of high availability or vulnerability. For example, after a night of heavy rain, we watched a male Roadside Hawk catch eight frogs at a newly refilled waterhole, and other Roadside Hawks hunted insects fleeing ant swarms. In two cases, Roadside Hawks caught a small rodent (from an 8 m perch) and a grasshopper (from a 3 m perch) that were fleeing fires in the slash-and-burn farming landscape.

Comments in the literature usually characterize Roadside Hawks as dietary generalists (Robinson 1994). In Argentina, based on 45 prey items, Beltzer (1990) documented a diet of insects and spiders (78%), frogs and toads (11%), fishes (7%), and rodents (4%), with one species of grasshopper comprising 51% of the diet. In one Argentinean study (Massoia 1988, data provided by A. G. Di Giacomo, pers. comm.) prey remains (guinea pig, *Cavia aperea;* thick-tailed opossum, *Lutreolina crassicaudata;* European hare, *Lepus capensis;* large opossum, *Didelphis albiventris*) were erroneously attributed to Roadside Hawks and probably were left by a larger raptor. At six nests studied at artificial forest openings in Guatemala, Vásquez and Reyes (1992) identified 52 prey items as 37% reptiles, 29% rodents, 15% birds, 17% insects, and 2% frogs; 1 item was unidentified.

The hunting behavior of Roadside Hawks from perches or occasional ground-walking and aerial attacks was typically buteonine Johnson and Peeters (1963) characterized the Roadside Hawk as *Accipiter* like and raised the question of whether this *Buteo* might participate in an unfilled *Accipiter* niche. We found no evidence of this, and records of birds in the diet are few.

This species is able to exploit a wide range of prey items and to successfully use many human-modified habitats. The dietary difference in the two habitats may reflect differences in the available prey base, but we have no data on the relative abundance of these prey types in the forest and farming habitats.

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Nutrient Preferences of Brazilian Hummingbirds

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ABSTRACT.—The Stripe-tailed Hummingbird (*Eupherusa eximia*) prefers nectar that is highly supplemented in both vitamins and minerals, when offered the choice of no, low, or high supplemented nectar. We tested the responses of hummingbirds in southern Brazil to four solutions: nectar, nectar supplemented with vitamins, nectar supplemented with minerals, and water with both vitamins and minerals added. Hummingbirds spent less time at and made fewer visits to the supplemented water than to the different nectar solutions, suggesting that nutrients alone are not enough to attract birds. One of eight species, the Violet-capped Woodnymph (*Thalurania glaucopis*), visited the mineral supplemented nectar more often than both nectars and one unidentified hermit species (*Phaethornis* sp.) visited the mineral treatment more than straight nectar. The Black-throated Mango (*Anthracothorax nigricollis*) made more visits to the vitamin supplemented nectar than to mineral-rich nectar whereas the Glittering-bellied Emerald (*Chlorostilbon aureoventris*) avoided the vitamin treatment, preferring straight nectar. A general pattern of preference was not found among species. *Received 11 Feb. 2000, accepted 23 Oct. 2000.*

The foraging strategies and energetic requirements of hummingbirds are well documented and it is generally accepted that they are energy limited (Montgomerie et al. 1984, Brice and Grau 1991). Foraging decisions of hummingbirds may be influenced by numerous factors, such as the energetic qualities of nectar (Montgomerie et al. 1984, Houston and Krakauer 1993), digestibility (Diamond et al. 1986), competition (Pimm et al. 1985, Tiebout 1993), predation risk (Lima 1991), and sexual dimorphism in bill morphology (Temeles and Roberts 1993). Abiotic factors might play important roles. For instance, ambient temperature affects thermoregulation and in turn, diuresis and the need to replace lost electrolytes (Calder 1979). Because the amount of energy in nectar is easily manipulated and quantified, most researchers working on the foraging ecology of hummingbirds have focused on the

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energetic benefits of different foraging strategies.

The importance of products other than carbohydrates in nectar as possible constraints on hummingbird foraging strategies has received little attention. Hummingbirds are believed to require various proteins, minerals, and lipids in their diet (Brice and Grau 1989, 1991). Nectar of specific flowers may contain all or a mixture of amino acids, proteins, lipids, antioxidants (including vitamin C), organic acids, alkaloids, glycosides, allantoin and allantoic acid, sodium, potassium, chloride, and other substances (Ziegler et al. 1964, Baker and Baker 1982, Hiebert and Calder 1983, Galetto 1995). Amino acids are present only in trace amounts. Adding them to nectar does not increase its attractiveness to hummingbirds in laboratory experiments, leading most researchers to agree that the birds use insects to complete their diet and obtain their amino acids (Hainsworth and Wolf 1976, Brice and Grau 1991, Stiles 1995).

In one of the first studies to examine the influence of nutrients on the foraging behavior of hummingbirds, Carroll and Moore (1993) showed that Stripe-tailed Hummingbirds (*Eupherusa eximia*) were significantly more attracted to artificial feeders that contained nectar supplemented with high levels of vitamins and minerals than to feeders with low levels or no additional vitamins and minerals. However, because the vitamins and minerals were presented in combination, it was unclear whether the hummingbirds were attracted by the high concentration of only one of the components (vitamins or minerals), or by an additional flavor created by the supplements. Our objective was to test the attractiveness of vitamin and mineral supplements separately in high concentration in nectar and together in water.

METHODS

We conducted this study from 7–13 January 1997 in Intervales Park (24° 16′ S, 48° 24′ W, elevation about 1000 m), São Paulo State, Brazil, in the Atlantic rain forest. We observed and monitored ten species of hummingbirds at our artificial feeders: female Amethyst Woodstar (*Calliphlox amethystina*), Black Jacobin (*Melanotrochilus fuscus*), female Black-throated Mango (*Anthracothorax nigricollis*), male Violet-capped Woodnymph (*Thalurania glaucopis*), Glittering-bellied Emerald (*Chlorostilbon aureoventris*), Sombre Hummingbird (*Aphantochroa cirrhocloris*), Versicolored Emerald (*Amazilia versicolor*), White-throated Hummingbird (*Leucochloris albicollis*), White-vented Violetear (*Colibri serrirostris*), and one hermit species (*Phaethornis* sp.) that could not be positively identified.

TABLE 1. Vitamin and mineral concentration used in experiments on nutrient preferences by Brazilian hummingbirds.

Vitamins	Quantity (/l)	Minerals	Quantity (/l)
A	1760 I.U.	Calcium	130 mg
D3	264 I.U.	Sodium	60 mg
E	2.84 I.U.	Zinc	2.5 mg
C	88 mg	Manganese	1.5 mg
B1	0.88 mg	Copper	0.65 mg
B2	1.76 mg	Iodine	0.015 mg
B6	2 mg		
B12	0.0044 mg		
K	0.44 mg		
d-Penthonic acid	4.8 mg		
Niacinamide	17.6 mg		
Choline	4.4 mg		

We suspended four 300 ml hummingbird feeders 2 m apart on a horizontal string 1.6 m above the ground in an open area, making it difficult for the birds to defend territories around our feeders. To control the position of hummingbirds while drinking, we blocked two of the three feeding apertures. We used liquid avian vitamins (Avitron; Lambert Kay™) and a mineral supplement (Avimin; Lambert Kay™) to create the different treatments.

Feeders were washed daily with mild soap, repeatedly rinsed with filtered water, and filled with 150 ml of one of the solutions. We used filtered water and cane sugar (5:1 by volume) as a basic nectar solution (control) and added either 6 drops of the vitamin or 1.5 ml of the mineral supplement (Table 1). To determine if the supplements alone were enough to attract hummingbirds, we filled one of the feeders with filtered water and the same concentrations of both vitamin and mineral supplements as we used with the nectar.

We randomly assigned feeder positions on the string and their contents each morning. The feeders were suspended at least one hour before the trials began to allow the hummingbirds to sample each feeder. We recorded the number and duration of visits of each species five times per day at 09:00, 11:00, 13:00, 15:00, and 17:00 CST. The four feeders were successively monitored during 5 min observation periods for a total of 700 min of observations. Although we observed ten species at our feeders, only eight made enough visits to allow statistical analysis. Therefore, we excluded Amethyst Woodstar and Black Jacobin from the analysis. We observed 580 min of feeding activity at the feeders.

We used analysis of variance (ANOVA) with duration of visit (log-transformed to satisfy the assumption

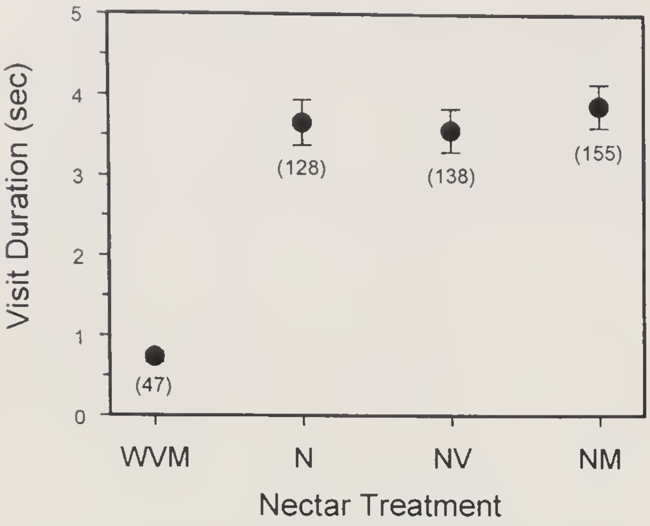

FIG. 1. Mean (solid circle) and standard error (verticle bars) of visit duration of Brazilian hummingbirds at four different nectar treatments; WVM: water supplemented with vitamins and minerals, N: nectar, NV: nectar supplemented with vitamins, and NM: nectar supplemented with minerals.

of normality) as the dependent variable and treatment, species, weather (no rain, light rain, heavy rain), and wind (none, mild, strong) as the independent variables to determine whether the duration of visits to feeders was influenced by supplementation with vitamins and minerals. Only independent variables that contributed to the variance were kept in the overall model; therefore, feeders ($F_{3,434} = 0.84$, $P > 0.05$) and their position ($F_{3,434} = 0.98$, $P > 0.05$) were discarded. We tested for preferences in the number of visits to the different nectar treatments for all species combined using χ^2 analysis. We used a contingency table to verify species effect. Because there was a species effect, additional χ^2 tests were performed on each species. We performed pairwise comparisons (using Tukey's method of correcting for multiple comparisons yielding confidence intervals) for each species that visited the nectar feeders unequally to find actual preferences. We set $P < 0.05$ for all tests, which were performed using S-Plus 4.5, Mathsoft© software on a PC.

RESULTS

We recorded 470 feeding bouts during the 580 min of feeding observations, only 5 of these bouts were interrupted by another bird at the feeder. The model for the duration of visits to the different solutions was highly significant ($F_{34,434} = 6.0$, $P < 0.001$) and duration varied significantly according to treatment ($F_{3,434} = 42.3$, $P < 0.001$) but this difference was attributed to the vitamin and mineral supplemented water treatment that the hummingbirds rejected (Fig. 1). Once we removed this treatment from the analysis, the model was still significant ($F_{26,395} = 2.3$, $P < 0.001$) but there was no significant effect of nectar treatment on visit duration ($F_{2,395} = 0.6$, $P > 0.05$). Duration of visit did not differ among the different species both with and without the water treatment included in the model ($F_{21,434} = 1.2$, $P > 0.05$; $F_{14,395} = 1.4$, $P > 0.05$; respectively).

The hummingbirds did not visit the different treatments with the same frequency ($\chi^2_3 = 59.0$, $P < 0.001$) and made fewer visits to the vitamin and mineral supplemented water. Once we removed the water treatment, difference in the number of visits per nectar treatment remained significant ($\chi^2_2 = 17.1$, $P < 0.001$). The nectar treatments were visited differently by the eight species ($\chi^2_{14} = 51.3$, $P < 0.001$). Therefore, each was tested for preferences (Table 2). One species (the hermit) visited the mineral-supplemented nectar significantly more often than unsupplemented nectar; whereas male Violet-Capped Woodnymph preferred the mineral-rich nectar over both other nectar treatments. In addition, female Black-throated Mangos visited the vitamin supplemented nectar significantly more often than the mineral supplemented nectar. Glittering-bellied Emeralds made more visits to the unsupplemented nectar than to the vitamin supplemented nectar. Although Sombre Hummingbird visited the nectar treatments unequally, it showed no significant preference. No other species exhibited any preference for any of the nectar treatments (Table 2).

DISCUSSION

Carroll and Moore (1993) found that Stripe-tailed Hummingbirds preferred highly supplemented (in both vitamins and minerals) nectar over low supplements and unsupplemented nectar. They attributed the preference to the high concentration of vitamins, but they also discussed the possibility that minerals and/or their flavor were the attractant. We found that vitamin and mineral supplemented water was less attractive to the hummingbirds than any of the nectar treatments, suggesting that the intrinsic value of the added nutrients, or their flavor, is not enough by itself to attract the birds.

Our inability to identify the sex for species without morphological sexual dimorphism is a drawback because gender could be an important variable determining condition and

TABLE 2. Number of visits made by each of eight species of Brazilian hummingbirds to artificial feeders containing different nectar solutions[a]. Differences among the treatments within each species were examined using χ^2 tests and when significant, pairwise comparisons using Tukey's correcting method for multiple comparisons, were performed to find preferences.

Species	N	NV	NM	P	P for the pairwise comparison
Versicolored Emerald	26	39	41	>0.05	
Black-throated Mango	21	35	19	<0.05	N-NV: >0.05 N-NM: >0.05 NV-NM: <0.05
Sombre Hummingbird	6	7	16	<0.05	N-NV: >0.05 N-NM: >0.05 NV-NM: >0.05
Glittering-bellied Emerald	21	5	13	<0.01	N-NV: <0.01 N-NM: >0.05 NV-NM: >0.05
White-vented Violetear	14	10	4	>0.05	
White-throated Hummingbird	16	13	5	>0.05	
Violet-capped Woodnymph	21	24	44	<0.01	N-NV: >0.05 N-NM: <0.01 NV-NM: <0.01
Hermit	3	5	13	<0.02	N-NV: >0.05 N-NM: <0.05 NV-NM: >0.05

[a] N: nectar, NV: nectar supplemented with vitamins, and NM: nectar supplemented with minerals.

consequently the choice of supplements. Barclay (1994) suggested that calcium is a major constraint on reproduction in bats and birds, and that the small clutches of hummingbirds are explained by their low calcium diet. Because nectar is a poor source of minerals, breeding females might forage differently than males; indeed, breeding female hummingbirds spend more time hunting insects than conspecific males (Stiles 1995). Insects are a good source of proteins and electrolytes, especially potassium (Hiebert and Calder 1983); their consumption could help females meet the demands of raising young (Stiles 1995). But insects are generally low in calcium and there are observations of hummingbirds, mostly females, eating mineral-rich compounds such as soil, wood ashes, and sand (Des Lauriers 1994, Adam and Des Lauriers 1998).

All the species we observed during our experiments were potentially breeding (Grantsau 1989) and females could have been calcium/mineral stressed. If so, then we would predict a preference for the mineral supplemented nectar treatment. Indeed, potential female hermits visited the mineral treatment significantly more often than nectar. Coincidentally, we found a female hermit nesting less than 300 m from our feeders. However, we cannot confirm whether we observed that nesting female or not because neither the species nor the sex could be determined and none of the individuals was marked. Male Violet-capped Woodnymph preferred the mineral treatment and female Black-throated Mangos visited the vitamin supplemented nectar significantly more often than the mineral supplemented nectar, similar to the preference of Stripe-tailed Hummingbirds observed by Carroll and Moore (1993).

Although our results are consistent with the breeding female/mineral stress hypothesis or a general preference for supplemented nectar, our results were mixed. Glittering-bellied Emeralds made significantly fewer visits to the vitamin supplemented nectar, preferring the nectar without any supplements. Three species exhibited no preference among the three sources of nectars in terms of the number or duration of visits. Our findings are unlikely to result from competition; we recorded few competitive interactions and small species such as Glittering-bellied Emerald had access to all supplements. The simultaneous observation of three to four birds per species in the vicinity of our feeders as well as the number and rate of visits per day suggest that we did not record only the preferences of a single bird of each species. However, because the birds were not marked we might have made multiple observations of some birds. This study highlights the need for further research on the requirements for products other than carbohydrates in the diet of hummingbirds. Such products might play a much larger role than is generally assumed in hummingbird foraging strategies. The ecological (e.g., temperature) and physiological (e.g., reproductive status) constraints affecting those requirements also need to be addressed.

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Great Horned Owl Death from Predation of a Toxic California Newt

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ABSTRACT.—We report the first records of the ingestion of a toxic California newt (*Taricha torosa*) and a particular species of Jerusalem cricket (*Stenopelmatus fuscus*) by a Great Horned Owl (*Bubo virginianus*). This is one of only a few records of avian predation on this genus of toxic newt. Ingestion of the extremely poisonous tetrodotoxin present in the newt's skin was likely the cause of the owl's death. *Received 11 April 2000, accepted 20 Oct. 2000.*

The Great Horned Owl (*Bubo virginianus*) is among the best known and broadly distributed of North American raptors. Primarily a nocturnal hunter from a perch, it occurs in many habitats, including forests, woodlands, swamps, orchards, and agricultural areas (Houston et al. 1998). Great Horned Owls are opportunistic foraging generalists and take prey that range from small insects to large birds (Marti and Kochert 1996). The food preferences of Great Horned Owls include mammals, birds, reptiles, amphibians, fish, insects, and various other invertebrates (Houston et al. 1998). Some birds commonly consume salamanders (Bent 1964). However, some salamanders, especially newts in the genus *Taricha* (Amphibia: Salamandridae), have toxic skin and warning coloration that should reduce or eliminate predation. Although natural predators of these taxa exist (Motychak et al. 1999), the only records of avian predation on *Taricha* are by juvenile Western Grebes (*Aechmophorus occidentalis*; McAllister et al. 1997), a Mallard (*Anas platyrhynchos*; Storm 1948), and domestic fowl (Pimentel 1952). None of these attempts at newt predation was successful and all of the birds died following ingestion.

On 24 January 1997, an adult female Great Horned Owl (*Bubo virginianus*) was found dead at the University of California Botanical Gardens in Berkeley. The owl's skeleton, stomach contents, and a frozen tissue sample are deposited in the Museum of Vertebrate Zoology (MVZ 179395). When the owl was dissected 23 November 1998, the proventriculus contained two food items, an adult male *Taricha torosa* (California newt; 70 mm snout-vent length) and a gravid female Jerusalem cricket (*Stenopelmatus fuscus*). This is the first record of a Great Horned Owl predation of *Taricha* and *Stenopelmatus fuscus,* though other local owls are known to eat this same species of Jerusalem cricket (Thomsen 1971). *Bubo virginianus* regularly consumes Jerusalem crickets (Stoner 1931, Earhart and Johnson 1970) but the crickets in Great Horned Owl stomachs have not been identified to species before. The newt recovered from the owl's stomach was in its aquatic breeding morph, having a laterally compressed tail, enlarged toe pads and smooth skin. In the vicinity of Berkeley, *Taricha* spp. migrate in large numbers to breeding ponds during the winter. The newt was oriented head first down the stomach and had puncture wounds that were presumably acquired when it was seized by the owl. Both the newt and the cricket showed no visible signs of digestion. However, the cricket was partially disarticulated with the head and one of the hind legs detached from the thorax.

Tetrodotoxin is among the most taxonomically widespread, highly potent, non-protein neurotoxins known and is characteristic of the genus *Taricha,* the most toxic of all salamanders (Brodie et al. 1974). This substance can kill avian predators within 2 minutes and debilitate a bird even sooner (Brodie 1968). Tetrodotoxin interferes with normal functioning of the nervous system and in sufficient quantities will produce hypertension and respiratory arrest caused by intense muscle paralysis (Fuhrman 1967). Given the absence of any

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other evidence for the cause of death (external bleeding, broken bones, bullet holes, etc.), the presence of the newt in the proventriculus and lack of significant digestion support the idea that the owl succumbed quickly to the poison. This situation parallels the presence of newts in the crops (Storm 1948) and stomachs (Brodie 1968) of other deceased birds. We hypothesize that the powerful and fast acting tetrodotoxin may not have allowed sufficient time or muscle control necessary for the owl to regurgitate the newt before respiratory failure and death.

In addition to its bright coloration, the species of *Taricha* distract or warn predators of their toxicity by vocalization (Davis and Brattstrom 1975) and body posture (Brodie 1977). These methods of predator evasion may not be effective against nocturnal predators. With such a large cost to eating highly toxic salamanders, the level of avian predation on the species of *Taricha* should remain low. Brodie (1968) noted that the toxicity of skin secretions in newts would not likely be selected for if it killed each predator that ate a newt. Nonetheless, avian ingestion of toxic salamanders is probably more common than is currently recorded because the location and dissection of deceased birds is an opportunistic practice.

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Ornithological Literature

Edited by Sara R. Morris

BABY BIRD PORTRAITS BY GEORGE MIKSCH SUTTON. By Paul A. Johnsgard. University of Oklahoma Press, Norman. 1998: 81 pp., 35 color plates. $24, hardcover.—Watercolor is a difficult, very spontaneous medium, but one that lends itself to effects generally unachievable with oils—such as making a downy chick truly appear soft and fluffy. George Miksch Sutton was a master at achieving this effect. This small volume is a collection of 35 color plates (one of which is only found on the back of the dustjacket) from the collection of the Field Museum of Natural History in Chicago. Five of the birds shown are adults, a few are in juvenal plumage, but most are either downy chicks or juveniles that still retain some juvenal down. The newly-hatched curlew (the chick on the back of the dustjacket) is a wonderful portrait with a habitat background; the others are simple portraits without backgrounds. Reproduction of these portraits is exceptional—particularly since many of the paintings have been considerably enlarged from the original, thus potentially showing flaws in the artist's workmanship. I suspect that Sutton would have insisted that they not be enlarged. Instead of flaws, however, the enlargement truly reveals the artist's skill.

Is this merely a beautiful picture book? No way! Sutton painted with a purpose. He painted to document the natal and juvenal plumages and soft-part colors of these birds and he has succeeded. Sutton prided himself on painting birds directly from life—really directly from life, unlike others who painted them from fresh specimens "shortly after life." While spending summers at the Edward S. George Reserve in Michigan, he studied development of plumages of several "sparrow" species, not only by monitoring nests, but also by raising young in captivity. Some of these paintings were published in Sutton's technical papers, others in popular articles published in Audubon magazine, but this is the first time they have been brought together in a publication. Dates and locations where the birds were painted are given in an appendix, but no captions other than Sutton's penciled annotations are provided with the plates. Plates 9 and 10, of young male Northern Cardinals (*Cardinalis cardinalis*) are reversed relative to the information in the appendix and are apparently not of the birds described in the text.

Text provided with each plate is an anecdotal portrait of interesting life history information that draws on Johnsgard's personal experiences with the species as well as Sutton's writings and the work of others. The text nicely complements the artwork and is typical "Johnsgard".—JEROME A. JACKSON.

COLLINS ILLUSTRATED CHECKLIST: BIRDS OF SOUTHERN AFRICA. By Ber van Perlo. Harper Collins, London. 1999: 320 pp., 84 color plates, numerous line drawings, 1228 range maps. $35.00 (Paper).—When Ber van Perlo's "Illustrated Checklist" for eastern Africa appeared in 1995 it created a stir. For the first time color illustrations of all the region's birds were brought together in a single, compact book. For many, the checklist quickly became the book of choice to carry into the field. Unfortunately, some deficiencies became apparent just as fast. Telegraphic text and tiny illustrations were acceptable in a "checklist," which made no pretence to be a fully-featured field guide. However, the text, illustrations and maps all contained significant sprinklings of errors—mainly minor—but misleading for the less experienced. Add a set of English names quite different to those commonly used in East Africa, and considerable confusion was (and continues to be) caused.

Now a southern African version has appeared, covering the region from Angola, Zambia, Malawi, and Mozambique south to the Cape. It looks and feels very similar to its sister volume and follows almost exactly the same format. A short introduction explains the book's coverage and the aspects (appearance, habits, habitat, occurrence and voice) that are treated in the text. Color maps of the region's climate, topography, and vegetation are a nice touch here. A set of 84 color plates follows, each with concise text on the facing page that describes the species illustrated. Next are the maps, one per species, an appendix of names in English, Portuguese, and Afrikaans, a brief bibliography and indices of scientific and English names—and that's it. The whole takes up 320 pages and produces a compact and very pocketable volume.

An "illustrated checklist" obviously stands or falls by its plates and these are remarkably impressive. Having had the east African avifauna to practice on, the author seems really to have got into his stride. Individual birds still look somewhat tiny, as there are often 20 species or more crammed onto a plate. However, the colors are much more realistic than before and the birds look infinitely more alive. Within tight constraints, van Perlo has done an excellent job of capturing "jizz". Some subtly plumaged groups such as greenbuls and illadopses are still shown with color contrasts that are (to be polite) wildly optimistic; others, like the nightjars, are just too scaled-down to show the plumage properly; but the overall standard is high. Successfully capturing this entire avifauna single-handed is quite an achievement. Comprehensive coverage of different plumages and birds in flight perhaps is too much to expect of an illustrated checklist. Nevertheless, van Perlo manages to fit in quite a lot of both, which is a bonus. Some of these illustrations should be particularly useful—for instance, the confusing canaries in flight on plate 83.

The text gives only the briefest and most essential information for identification. The names come from "Birds of Africa" and Dowsett and Dowsett-Lemaire's list; birders from the region will find familiar southern names in brackets where appropriate. Habitat is succinctly described for all species, and voice for the vast majority. The notation of voice may seem idiosyncratic, if not downright peculiar, but it is actually done with considerable care and precision. The text indicates "uncommon" or "rare or vagrant" species (dropping the colored numbers on the plates used for the eastern African book), while the maps have three shades of grey to show relative abundance. I found these shadings hard to differentiate, but practice might help. "Odd" records are indicated on the maps by crosses (which are not conspicuous and need some concentration to pick out). These are now distinguished from isolated populations, which appear as a star shape—a useful innovation. Although the maps show the whole southern third of the continent, ranges are only shaded in for the countries covered in the book, which I find distracting. It can take careful scrutiny to tell whether a place is out of range for the bird or just for the book.

The maps also show status for southern Africa's many migratory bird species. This complex 13-way classification no doubt reflects the messy reality but is not at all easy to assimilate at first reading. I may eventually be able to tell apart W(S) [winter visitor mainly, some stay in summer] and (SW) [mainly resident, partly all-year visitor] but I suspect it could take some time. Every map now has the species' name beneath it, not just its number, which is a vast improvement—no more tedious leafing back and forth from map to plate when you can't remember what, say, 69.16 refers to. Unfortunately, this to-ing and fro-ing is still necessary when the text opposite some plates overruns—a nuisance, but presumably unavoidable.

How accurate is the information? In contrast to the eastern African checklist, no obvious mistakes leapt off the page. This might be because I don't know these southern birds as well, but it does seem as though both author and publisher have paid more careful attention to the details this time around. There are a few little things—map 54.5 for example, is actually for the Black-winged Oriole (*Oriolus nigripennis*) not the Black-headed Oriole (*O. larvatus*) but they do seem very minor.

In eastern Africa, the illustrated checklist sprang into an open arena—there was, at the time, a dearth of decent bird identification guides for anywhere in the region. The situation is quite different down south where several first-class guides continue to slug it out, in continually improved and updated versions, for the birding market. Being already spoiled for choice, what might attract the southern African birder to van Perlo's book? For anyone whose birding interests resolutely stop at the Zambezi or the Angola border, probably not a lot (though it is a compact alternative to carry to the field). However, van Perlo covers a geographic area some half as big again as other southern African guides. This wider scope takes in about a third more bird species, too (1227 in total, plus another 45 on plate 84, a mouth-watering little extra that crams in rainforest species from Cabinda, Angola's tiny enclave between the two Congos). While there are already supplementary guides published for Zambia and Malawi, van Perlo's is the only single volume to cover these countries; for Angola and northern Mozambique, there's simply nothing else that is remotely up to date or portable, let alone illustrated in color. In fact, a lot of the Angolan birds have probably never been adequately illustrated before and it's exciting to see them depicted here. For any of these countries, this book is strongly recommended.

Perhaps only the most intrepid birder is likely to venture to some of these places at the moment, but clearly there are lots of wonderful species waiting to be seen. If nothing else, I am certainly going to enjoy this book as an armchair birder. If you have any interest in exploring the wonderful diversity of African birds, it is worth adding this colorful and inexpensive volume to your shelf.—LEON A. BENNUN.

BIRDS OF AFRICA: FROM SEABIRDS TO SEED-EATERS. By Chris and Tilde Stuart. The MIT Press, Cambridge, Mass. 1999: 176 pp., numerous color plates, two maps. $29.95 (cloth).—According to its dust jacket, this attractive and readable book is 'neither a field guide nor a biological text'. Just what it actually *is* seems harder to define. Essentially "Birds of Africa" is a semi-popular, family-by-family overview of the continent's avifauna. For each group it gives an outline of diversity in the world and in Africa, general information about biology and behavior, and a few notes on conservation. Most accounts are a page or two long, and include some good-looking color photographs; scattered here and there are boxes of more detailed information on miscellaneous topics such as "Birds in the rainforest," "The mystery of the Congo peacock," "Threats to migrants" and so on.

Does it work? Sort of. Rather than the families appearing in taxonomic order, they are clustered under other headings: "Terrestrial birds," "Hole nesters," "Sandgrouse, doves and fruit-eaters," "Coucals and brood-parasites" and even "LBJs" (a dumping ground for larks, bulbuls and all the warblers, among others). There's nothing wrong with this in principle, but it does make for a rather confusing and jumbled arrangement; some families could equally well belong in several categories, the headings mix in feeding, nesting, habitat, and identification (LBJs is hardly an ecological label!), and of course evolutionary relationships are obscured.

The family accounts themselves are clear and interesting. The authors have done their homework well, but in a few paragraphs they can only give a bare outline of each family's characteristics. Details would have to be found elsewhere. Sometimes this is a little frustrating—for instance we are told (p. 60) that there are only five true partridges in Africa, but what, beyond the name, makes a true partridge? I found the prose style a little flat and monotonous, though certainly readable enough. It is pleasantly jargon-free and enlivened on occasion by the authors' own observations and anecdotes. The numerous color photographs are all well reproduced and pleasing to the eye, but only sometimes link directly to the species mentioned in text. Some families, like the broadbills, pittas, and painted-snipes, don't seem to merit a picture at all. The authors have decided to cover the entire African continent, rather than the Afrotropics *per se,* which means that Palaearctic families such as wrens, accentors, wall-creepers, and waxwings (which only creep in to extreme North Africa) have their own accounts. Perhaps it would have been better instead to expand the treatment of some large Afrotropical groups, such as warblers and flycatchers, which receive only cursory treatment.

The text boxes deal with an idiosyncratic range of topics but are informative, if you can find them. They are not indexed anywhere, so tracking them down is not easy. The text gives no references and no scientific names, but near the back there is a short list of suggested reading and a long list of all the birds of Africa. It's not clear what the African list is based on. The names seem to come from the treatment by Sibley and Monroe, but the arrangement of families certainly does not, and contains some oddities: tribe and subfamily labels are scattered about randomly and inconsistently; the monarchs and batises are thrown in with the Muscicapidae and so on. The English names here do not match those in the text and pictures, which is very confusing. None of the three warblers captioned on p. 127 appears in the species list, for example (the captions give their southern African names instead), and the reader will also search in vain for the two *Pycnonotus* bulbuls illustrated on p. 122.

There are other places where the authors don't quite get it right. The introduction states that birds evolved from pterodactyls—not a widely held view! The Sokoke Pipit (p. 125) is not restricted to coastal Kenya (it occurs in Tanzania too). The box on "Threats to migrants" concentrates misleadingly on just those from the western Palaearctic, ignoring the eastern flyway whose birds show different migratory behavior and timing. The threat codes that are shown in the species list are based on a categorization and classification that has been obsolete since 1994.

Despite these small shortcomings, the book succeeds in what seems to be its main aim: giving an agreeable and attractively illustrated overview of Africa's avifauna. Any Africa-based birder who is starting to move beyond species identification and develop a wider interest would find it accessible and useful. More experienced ornithologists might find that it does not repay their investment.—LEON A. BENNUN.

HARMONY AND CONFLICT IN THE LIVING WORLD. By Alexander F. Skutch. University of Oklahoma Press, Norman, Oklahoma. 2000: 288 pp., 18 b&w illustrations. $24.95 (cloth).—Paradoxes in nature are the focus of Alexander Skutch's latest book, particularly how harmony, critical to the internal health of organisms, gives way to strife in those organisms' external relations. This set of connected essays touches upon aspects of incongruities of nature, how organisms exemplify these incongruities, and our attitudes toward these incongruities.

As advertised, this is a thought-provoking book, and Skutch wrestles with the paradox of carnivorous plants and the loss of instinct during the growth of intelligence. He also examines unpopular approaches to understanding paradoxes, such as teleology, anthropomorphism, and group selection. Throughout, he emphasizes cooperation and harmonization, attributes he feels are long-overlooked and overshadowed by exploitation and conflict.

The introductory essay outlines the major and minor paradoxes that will be explored throughout the book. Here, Skutch presents his argument that the integument surrounding living things forms a physical and psychological boundary that allows organisms to be removed from their environment and other organisms. Interactions inside this boundary are cooperative and harmonious, while those outside are primarily those of conflict. This principle of harmonization is denoted as the driving force of evolution, as opposed to the "dreadful embroilment into which the living world is plunged by the manifold interactions of evolutions products". Harmonization occasionally prevails over conflict in the natural world, and the author gives many examples of cooperation among animals, including how morality plays a role in human relations.

Tackling both the species concept and the idea of selfish genes, the author considers explanations whereby individual actions promote the propagation of its species, or at least its deme rather than just its own lineage. In this light, genes, rather than being selfish, appear to be altruistic. Explanations for birds singing a variety of songs in different parts of its territory (pure enjoyment or sexual selection on repertoire size) or feeding a heterospecific nestling (being moved by the chick's pleas) are proffered as alternatives to harsher explanations.

The following essays explore in depth how contrasting impulses can coexist in animals. Hunger, fear, and sexual rivalry are precursors to hostility that arise from ultimate harmonious impulses such as aggregating for food or mates. In the exploration of how domestication influences this two-fold nature, particularly in humans, the author maintains `that friendly or integrative attitudes are more fundamental characters of animal life rather than hostile or disruptive ones. Skutch presents a diagram of animal nature (including humans) whereby basal attributes are harmonious and creative, secondary nature attributes are aggressive and selfish (as a consequence of natural selection in the predator-prey arena), and tertiary nature attributes are a mix of the primary and secondary and are influenced by society.

The next essays present a multitude of examples of mutual aid and cooperation in natural systems, including mutual protection in birds and mammals (warning behaviors, calls, safety in aggregation). As students of biology can list many examples of exploitation, the author emphasizes cooperation (mainly passive among plants, although he does mention tree/mycorrhizae symbioses), particularly among the vertebrates he knows so well. Examples here focus on work on highly social birds (Groove-billed Anis [*Crotophaga sulcirostris*], Australian Wood-swallows [family Artamidae], White-cheeked Colies) to describe the apparent lack of compromise between social and anti-social tendencies. Cooperative behaviors observed include preening in pigeons, parrots, anis, and Marbled Wood-Quails (*Odontophorus gujanensis*), various social feeding scenarios, such as mixed woodland feeding flocks, mate-feeding, and literature references of companion-feeding of injured birds (pelicans, boobies, crows, frigatebirds, wood-swallows). This diverse list is grist for Skutch's mill—that cooperation is widespread and should receive as much attention in any evolutionary philosophy as competition. The chapter closes with an optimistic view of humans, labeling our spiritual and intellectual development, despite the restrictions of our flexible but insulating integument, as most unpredictable—the greatest paradox.

I found the essay on carnivorous plants to be more of a treatise on the more than 450 plants that have adopted this way of life—a lot of detail and without the stimulating quality of the other chapters. This chapter stood apart from the rest of the essays; its inclusion, while providing details on the perplexing paradox of these plants, detracted from the collection as a whole. I was glad to get back on more philosophical ground in the following chapter addressing what Skutch refers to as "biological heresies".

The essay addressing these heresies was particularly insightful and interesting, with the author outlining unconventional points of view. He suggests that cries of anthropomorphism when interpreting animal behavior are due to a disconnect between recognizing morphological and behavioral evolution. Recognizing psychic similarities, Skutch argues, is just an extension of recognizing morphological similarities. Arguments against teleology, Skutch argues, stem from a misunderstanding between ends and purposes. Ends are often the result of processes, which is subtly different from attributing purpose to actions. Skutch argues most strongly for the acceptance of group selection and against the primacy of individual selection. He suggests that the latter exaggerates the self-sufficiency of the individual, neglects social interactions, and underestimates the complexity of evolution, using mate choice in birds, particularly in species with bi-parental care, and cooperative breeding, as examples. These viewpoints raise interesting questions about how we view evolutionary topics as well as how we pursue truth.

In the essay on conservation, Skutch presents a strategy for conservation that promotes biocompatibility over biodiversity, whereby more destructive, less contributing, or less connected species would not warrant protection. Fans of predatory vertebrates may wince at the outline of this approach. This point of view certainly flies in the face of present conservation practices and thinking and requires, as the author rightly points out, a detailed understanding of the ecosystems with which we are dealing.

The final chapter explores the relationship between instinct and intelligence and how the transfer from the former to the latter has been complicated and difficult. For humans, controlling ourselves is difficult and nascent intelligence needs spirituality to rise above the conflict. In this essay and the epilogue, the author reiterates his point about how the integument enables external conflict, but he ends on a hopeful note for humanity—the most successful product of evolution and harmonization. If spiritual and intellectual development can override conflict among humans, the species can survive.

I recommend this book for students of ecology, behavior, and evolution, particularly in its impassioned treatment of ideas out of the mainstream. Alternative viewpoints are the stuff of scientific inquiry; Skutch provides much of the former based upon a lifetime of practicing the latter.—THOMAS GOOD.

HOPE IS THE THING WITH FEATHERS. By Christopher Cokinos. Jeremy P. Tarcher/Putnam, New York, New York. 2000: 360 pp. $24.95 (cloth).—In *Hope Is the Thing With Feathers,* author Christopher Cokinos presents intriguing accounts of the lives and deaths of six extinct species (or races) of North American birds. As may be surmised from the title, which is taken from an Emily Dickinson poem, this is not a scientific work; rather, it is written for a lay audience. Information is presented on the basic natural history of each species (such as it is known), the historical context surrounding its extinction, and the specific events that led to its decline and ultimate extinction. Cokinos also includes his personal experience, such as a sighting of a similar species or a trip to the site of the death of the last known individual, as well as his reactions to the loss of species. The historical portions are engagingly well written and the text is interspersed with some fascinating photographs and plates, many rarely or never before published.

The book is divided into major sections on each species, each with one to three chapters. In the first chapter on the Carolina Parakeet (*Conuropsis carolinensis*), the author describes his sighting of a pair of escaped Black-hooded Conures (presumably *Nandayus nenday*), brilliant green and out of place over a Kansas marsh in autumn. In his subsequent reading on this species, he learned that there had in fact been bright green, tropical looking psittacids in Kansas, and in the winter even. He details how this realization and his fascination with species gone forever set him off on the 10 years of research that resulted in *Hope Is the Thing With Feathers.* Similar personal narratives are interwoven into the chapters on the Ivory-billed Woodpecker (*Campephilus principalis*), Heath Hen (*Tympanuchus cupido*), Passenger Pigeon (*Ectopistes migratorius*), Labrador Duck (*Camptorhynchus labradorius*), and Great Auk (*Pinguinus impennis*).

In the introduction (p. 3), Cokinos points out that "Perhaps unlike a professional historian and more like the poet I have been, I found myself drawn to the oddments, the margins, so that a cookbook's reference to Passenger Pigeon pie looms as importantly in this book as, say, logging statistics. A settler's account of how Carolina Parakeets in sycamores reminded him of Christmas trees in Germany—that matters to memory as much as facts of biology." A strength of the book is the manner in which Cokinos is able to interestingly present both the seemingly insignificant, such as the observations of early settlers, and the most current biological theory and knowledge (including a competent discussion of the generalized extinction process for the lay reader, with distinction between proximate and ultimate causes). I also enjoyed the stories of efforts by early conservationists and ornithologists, such as the search for Ivory-billed Woodpeckers at the Singer Tract in Louisiana by Arthur Allen, Peter Paul Kellogg, James Tanner, and George Sutton.

Excepting a reference to the use of rifles by early specimen collectors (the shotgun was the weapon of choice), I found few inaccuracies and have few criticisms. Mention is made of a stop to record Wild Turkeys (*Meleagris gallopavo*) at "the Stoddard plantation" in Georgia by the team mentioned above. Presumably this was the plantation of Herbert Stoddard, the great quail and turkey biologist, and it seems odd, particularly in the context of this story, that no more detail was offered on such a gathering of great ornithologists. Also, I occasionally found some of the accounts of the author's personal experiences as well as some of the philosophical reflections to be a bit long and tedious.

Cokinos suggests that "we must redefine hope from wish to work". In his book *Deep Enough for Ivorybills,* James Kilgo (1988, Algonquin Books of Chapel Hill, Chapel Hill, North Carolina) relates how, as a child in the 1950s his family would travel to the beach and en route, cross the wide floodplains of South Carolina's rivers. Referring to the extensive bottomland hardwood forests, his father would say "I bet there're still Ivorybills in there." We all hope that an Ivory-billed Woodpecker or a Bachman's Warbler (*Vermivora bachmanii*) will again turn up, but since they almost certainly will not, the message of Cokinos' book is that we must do more than hope; we must act to prevent the extinction of the species we still have. An important step in this process is remembering the species and learning from the mistakes that led to their extinction. In this capacity, *Hope Is the Thing With Feathers* will be an important and, hopefully, enduring book.—JOHN C. KILGO.

STURKIE'S AVIAN PHYSIOLOGY. Edited by G. Causey Whittow. Fifth ed. Academic Press, New York. 2000: 685 pp., numerous tables and b&w illustrations, index. $ 99.95 (cloth).—This is the first edition of *Avian Physiology* that Paul D. Sturkie, Professor Emeritus at Rutgers University, neither edited nor wrote any of the contents. In its many editions, *Avian Physiology* has been a standard reference on the topic for ornithologists; this edition will be no exception. Many of the chapters are written by new authors and the material differs considerably from the previous edition. There are new chapters on flight, incubation, and development and growth. There are also some chapters missing, most obvious are the ones on metabolism and on the integument. Some of the information on metabolism has been incorporated into other chapters but most of it is no longer included; the same is true for the material on the integument. Wild birds are covered as well as domestic species, although for some topics much more is known about domestic species.

The flow of the book is similar to previous editions: sensory and central nervous system, motor control, musculature, respiration, excretion, gastrointestinal, flight, endocrinology, reproduction, and immunophysiology. Each chapter is independent and has its own figures, tables, and references. Putting the references at the end of each chapter makes it faster to look up a citation and much easier to scan a list of relevant citations. The quality and usefulness of the illustrations are good and appropriate. There were two features of the book that I found to be unsatisfactory. The most important is that most of the chapters seem to have been written in 1995; I found few 1995 literature references and none after that date. For a book with a publication date of 2000, that seems to be an extraordinary delay in publication. The second is the elimination of information that was present in the previous edition. This was probably an editorial decision to keep the book's length from becoming too long but the result is that having copies of both editions is almost a necessity. Although the book is intended to be used as a text for avian physiology courses, it makes an excellent single-volume reference of the subject. For most ornithologists and ornithology graduate students, it will be a valuable resource.—ROBERT C. BEASON.

STARLINGS AND MYNAS. By Chris Feare and Adrian Craig. Princeton University Press, Princeton, New Jersey. 1999: 285 pp., 32 color plates and distribution maps, bibliography, index $39.50 (cloth).—This book is a comprehensive guide to all 114 species of the starling family (Sturnidae). Well-written introductory chapters include a general introduction to each genus, and current information on phylogenetic relationships among the genera. Although some species, such as the common starling, are well known around the world thanks to introductions, others are fairly rare. This means that classification of this family is continuing to change. In fact, Feare and Craig offer a revised intra-family classification based on current behavioral data. The general descriptions of habitat, social behavior, and mating behavior drive home the authors' point that this Old World family is very diverse. Starlings occupy habitats from rain forests to deserts, and grasslands to forest canopies. Their social and mating systems are also varied; some species are considered relatively solitary breeders, others are gregarious, and still others live in large colonies and breed cooperatively.

There is a very interesting section on "Starlings and Man". The most common of these birds are well known to people because of their interesting vocalizations and their ability to successfully nest in man made structures. Interestingly, starlings are known as both pests and beneficial organisms for some of their other habits. For example, many species are flexible enough to be able to take advantage of transient food sources such as locust swarms. Unfortunately they are also good at finding seasonally available agricultural food sources such as cherries, grapes, and olives. From a conservation standpoint, an important aspect of human impact on this family is the many introductions of starlings that have occurred. Some species were introduced into areas as agents of biological control and some for aesthetic reasons. Research in some regions of introduction demonstrate that these birds can take a toll on populations of native species that do not successfully compete for nesting sites and other resources. On the other hand, at least 5 species of starlings are known to have become extinct, 7 are globally threatened, and an additional 15 are near-threatened. The major cause of these threats is loss of habitat and capture of birds for aviculture.

The bulk of this book (212 pages) is devoted to color plates, distribution maps, and descriptions of each species. The illustrations are wonderful, beautifully capturing even the iridescent plumage colors of these birds. Where appropriate, individual illustrations of males, females, and individuals of subspecies are depicted. The detailed species accounts include field identification and basic description, measurements, voice, distribution and population notes, habitat, and information on feeding, breeding, and other behavior.

Overall this book piques one's interest in this diverse group of birds, and will be a useful addition to the library of ornithologist and world-traveller alike.—MARTA HERSEK.

BIRDING IN THE AMERICAN WEST. By Kevin J. Zimmer. Cornell University Press, Ithaca, New York. 2000: 402 pp., numerous black-and-white photos and illustrations. $25.00 (paper), $49.95 (cloth).—As the author says, this book is "intended as a companion handbook to aid in finding and identifying birds in the American West." The coverage includes all of the western United States from "the eastern boundaries of the Dakotas, Nebraska, Kansas, Oklahoma, and Texas westward, including Alaska". It does not include Hawaii.

The first three chapters give some general, but useful, discussions of how to find and identify birds and how to keep useful field notes on them. If I were to give one single piece of advice to a beginning birder, I would tell them to keep a log of all field trips. Zimmer's chapter on notes is a useful description of how to do this correctly. A record of locations, weather, time spent, and numbers of each species can, over time, become extremely useful. For old guys like me, such records also serve as reminders of bird trips and other adventures that we remember with difficulty or imperfectly. Furthermore, one of the rarest of data sets is a long record of the birds of any given location kept by a careful observer skilled in keeping notes and who has been in the field a lot. Zimmer's general sections on finding and identifying birds may not be as useful to an experienced birder, but I learned a number of good things.

In the remaining chapters (and the bulk of the text), the book deals with specific identification problems. This includes how to separate the species of loons, dowitchers, hawks, the difficult gulls, finches, thrashers, hummingbirds and many more such problems. I found the parts on identification extremely useful and accurate. Most birders will find something here to add to their techniques for separating difficult birds. Personally, I never seem to have time to really check out the criteria for separating birds like Pacific Loons (*Gavia pacifica*) from Arctic Loons (*G. arctica*) and Common Loons (*G. immer*). Zimmer's book helped me out with these and several other "toughies".

Zimmer's coverage on bird finding will not replace publications on birds in specific locations (e.g., ABA Lane Birdfinding guides and the like), but appeared to be useful in at least a general sort of way. In a few instances in which I had first-hand knowledge of bird occurrence (e.g., western Montana), I found the "finding" part slightly misleading (although not in any way that severely detracts from the text or in eventually finding specific birds). On the other hand, if I had read this book before my most recent Texas trip, I would have known exactly where to find Nelson's Sharp-tailed Sparrow (*Ammodramus nelsoni*). Zimmer gave both locality and habitat precisely.

The line illustrations are clear, helpful, and very professionally presented. The photos show what is claimed and are very useful. The paperback version seems sturdy and should survive extensive fieldwork. The author should be congratulated as he has produced a book that has succeeded in being informative, readable, and helpful. I recommend it to anyone birding in the western states.—C. R. BLEM.

TAKING WING: *ARCHAEOPTERYX* AND THE EVOLUTION OF BIRD FLIGHT. By Pat Shipman. Simon and Schuster, New York, New York. 1998: 336 pp., 77 numbered text figs., bibliography, index. $25.00 (hardbound).—This is a book that should be of value to all ornithologists, paleontologists, evolutionists, and indeed anyone who is just plain interested in fossils and how scientific ideas are formulated, re-formulated, argued, and re-argued over and over again, as new evidence emerges and old data is reevaluated. The story of *Archaeopteryx* is a timeless classic.

Written for a general audience, TAKING WING is definitely a good read. The book opens with a fascinating description of the discoveries of the specimens (seven partial skeletons, the most recent having been found in 1992, and an isolated feather) known to science as *Archaeopteryx*, which at approximately 150 million years old was (in the 1860s, when first recognized) and is still the oldest known undisputed bird (or more technically, we might say "bird-like form", or a member of the Avialae, since not everyone considers it a true member of the Aves). In the 1860s Thomas Henry Huxley proposed, on the basis of his studies of *Archaeopteryx*, that birds and dinosaurs are closely related, and indeed the bulk of evidence, as recounted by Shipman, has only strengthened that assessment over the intervening years. Demonstrating just how close birds and small dinosaurs are in their gross overall morphology, a couple of *Archaeopteryx* skeletons were originally misidentified as the small dinosaur *Compsognathus*, and the first *Archaeopteryx* specimen found (in 1855) was classified as a pterodactyl until finally recognized for what it was by John Ostrom of Yale in 1970.

In the course of her book, Shipman adroitly discusses various aspects of both avian and non-avian flight mechanics (including pterosaurs, bats, insects, and "gliding" animals such as "flying" fish, gliding lizards, and "flying" squirrels), functional morphology, and comparative anatomy. She addresses the classic question of whether bird flight started from the ground (running, flapping, and ultimately flying) or from a height (gliding and then flying). She also covers behavioral attributes, such as nesting behaviors in dinosaurs and birds, and physiological considerations—for instance, the question of "warm-blooded" dinosaurs. Perhaps most importantly, Shipman works through the maze of cladistic analyses pertaining to avian relationships with a minimum of jargon and a sense of balance. She briefly details the various theories of avian ancestry: Are the closest relatives of birds found among primitive pseudosuchians (primitive or "ancestral" archosaurs), theropod dinosaurs, crocodylomorphs, or possibly some other form? As Shipman points out, the proponents of either a primitive pseudosuchian or crocodylomorph hypothesis have criticized the detailed cladistic analyses of the dinosaur-avian proponents, but they themselves have failed to counter with comparably detailed analyses supporting their own hypotheses. As TAKING WING was completed the weight of evidence supported a close dinosaur-avian relationship. Simplistically, terrestrial bipedal theropod dinosaurs, covered with insulating "feathers", chasing small prey with their forelimbs, ultimately evolved into flying birds with flapping wings.

Scientific discoveries do not stop, and so new fossils have been found bearing on the origin of birds and flight since Shipman completed her book—and, on the whole, they strengthen the close affinity of theropod dinosaurs and birds. It now seems established that theropods commonly bore feathers during at least some stages of their lives. Among new discoveries, we might mention the Chinese forms *Sinornithosaurus millenii* and *Protarchaeopteryx robusta*, both considered in some ways intermediate between dinosaurs and birds; and *Beipiaosaurus inexpectus* and *Cau-*

dipteryx zoui, dinosaurs with feathers (or are they birds?). And then there is the tawdry tale of the premature announcement, under the auspices of the National Geographic Society (the same group that previously announced the discovery of a 225 million-year-old fossil dubbed *Protoavis* that, as it turned out, was based on such scrappy material its affinities, much less any possible birdlike features, are ambiguous at best—accordingly, most experts have virtually ignored *Protoavis*), of the new 125 million-year-old fossil "bird" from China dubbed *Archaeoraptor liaoningensis* in late 1999. *Archaeoraptor* was hailed as having the shoulder girdle and breast bone of a modern bird but a dinosaur-like tail. By early 2000, retractions were being issued stating that the specimen, which had been purchased on the open fossil market, is actually a natural (that is, it was not purposefully faked) composite of at least two different individuals: an early toothed bird (which is new to science) and the tail of a dromaeosaurid (a group within the theropods) dinosaur. Perhaps one of the lessons of this minor scandal is that early birds and certain early dinosaurs are, as Huxley espoused just after Darwin published *On the Origin of Species,* almost indistinguishable. Final conclusion: The dinosaurs never really went extint; we know them as birds and all the ornithologists of the world are really dinosaurologists. This thought should warm the heart of any paleontologist, including the one writing this review.

What about the question: Could *Archaeopteryx* fly? Over the years, some researchers have questioned whether it could actually fly or possibly just glide down from a high perch. Shipman concludes that not only did *Archaeopteryx* fly, but it could take off from the ground. In this sense it was a true bird that could "take wing".—ROBERT M. SCHOCH.

Wilson Bull., 112(4), 2000, pp. 575–583

PROCEEDINGS OF THE EIGHTY-FIRST ANNUAL MEETING

JOHN A. SMALLWOOD, SECRETARY

The eighty-first annual meeting of the Wilson Ornithological Society was held Wednesday, 26 April, through Sunday, 30 April, 2000, at the Hotel Galvez, Galveston, Texas, in joint session with the Association of Field Ornithologists. The meeting was sponsored by the Houston Audubon Society and the Gulf Coast Bird Observatory; Dwight Peake chaired the local committee.

The Council met from 13:12 to 19:29 on Wednesday, 26 April, in the West Parlor of the Hotel Galvez. That evening there was an informal reception for the conferees and guests on the Hotel Galvez veranda.

The opening session on Thursday convened in the Music Room at 08:34 with welcoming remarks from Dwight Peake, president of the Gulf Coast Bird Observatory. He, in turn, introduced WOS President John Kricher and AFO President Jerry Jackson, both of whom also welcomed those in attendance and provided the latest conference information. Jed Burtt then introduced the fourth annual Margaret Morse Nice Plenary Lecture, "Behavioral studies of chickadees and other species," presented by Susan M. Smith.

The scientific program included, in addition to the Nice lecture, 65 contributed papers and 16 contributed posters, which were organized into six paper sessions, a poster session, and a symposium on weather radar and its application to ornithology. The committee on the scientific program was chaired by WOS Second Vice-President Charles Blem. The radar symposium was coordinated by Daphne Gemmill and John Black.

The evening program on Thursday included a reception, followed by the AFO and WOS business meetings. Several all-day field trips were scheduled for Friday, including visits to Bolivar Flats, High Island, Anuahac, Galveston Island, the Quintana, San Bernard NWR, GCBO Headquarters, and the Brazoria NWR area. Conferees also enjoyed great local birding on trips scheduled before paper sessions on Thursday and Saturday, including a visit to one of the last two remaining active leks of the Attwater's Prairie Chicken. Half-day and full-day birding trips were scheduled for Sunday, as well.

The attendees enjoyed a sixty-minute social gathering prior to the annual banquet, which was held in the Music Room of the Hotel Galvez. After a fine dinner, President Kricher delivered a few brief remarks to the society. The following awards and commendations also were presented:

MARGARET MORSE NICE MEDAL

(for the WOS plenary lecture)

Susan M. Smith, "Behavioral studies of chickadees and other species."

EDWARD'S PRIZE

(for the best major article in volume 111 of *The Wilson Bulletin*)

J. Christopher Haney, "Hierarchical comparisons of breeding birds in old-growth conifer-hardwood forest on the Appalachian Plateau." Wilson Bull., 111(1):89–99.

LOUIS AGASSIZ FUERTES AWARD

David C. Lahti, "Testing behavioral evolution in response to ecological change in the Village Weaverbird."

GEORGE A. HALL/HAROLD F. MAYFIELD AWARD

(formerly the Margaret Morse Nice Award)

Emile Snell-Rood, "Assessing the success of created forest wetlands in southeastern Virginia through ornithological research."

PAUL A. STEWART AWARDS

Danielle E. D'Auria, "The breeding biology and social system of a desert adapted species, the Chihuahuan Raven."

Sarah L. Hamilton, "Ecology and body condition of the Northern Saw-whet Owl and Flammulated Owl during fall migration."

Kendell Daly Jenkins, "The role of diet and molt in determining the spring departure date of the White-throated Sparrow."

Eric L. Kirshner, "Survival and dispersal of juvenile Eastern Meadowlarks."

WILSON ORNITHOLOGICAL SOCIETY TRAVEL AWARDS

K. A. Baum, "The significance of color cues for hummingbird foraging patterns."

C. Field, "The role of subcolonies in a Least Tern colony in Massachusetts."

E. D. Fink, "Habitat use and reproductive success of shrubland songbirds in the Missouri Ozarks."

K. Flaagan, "Nest-site selection of the coastal Cactus Wren *Campylorhynchus brunneicapillus* in Chino Hills State Park, California."

V. Hake, "Radio waves from VHF transmitters and the effect on homing ability in *Columbia livia*."

L. B. Martin, "Woodpecker snag preference in a managed Virginia hardwood forest."

J. R. McCormick, "Delayed reproduction of reintroduced Red-cockaded Woodpeckers."

R. Nagarajan, "How do oystercatchers (*Haematopus ostralegus*) increase their intake rate?"

D. W. Podlesak, "Factors affecting the growth and survival of nestling Prothonotary Warblers in Virginia."

V. Shafer, "A phylogenetic analysis of cooperative breeding in the class Aves."

K. A. Wohlfort, "Time-activity budgets of non-nesting Common Loons in New Hampshire during the breeding season."

ALEXANDER WILSON PRIZE

(for best student paper)

A. N. Chadwick, "Within-site selection of artificial cavity trees by Red-cockaded Woodpeckers."

C. Audra Bassett, "Habitat selection of the Swainson's Warbler."

LYNDS JONES PRIZE

(for best student poster presentation)

Cheryl Pierce, "Distribution of Bicknell's Thrush (*Catharus bicknelli*) in the Catskill Mountains of New York."

Selection committee for the Nice Medal—Edward H. Burtt, Jr. (Chair), Charles R. Blem, William E. Davis, Jr., and John C. Kricher; for the Edwards Prize—Robert Beason (Chair), Sheila Conant, and Sara Morris; for the Fuertes, Hall/Mayfield, and Stewart Awards—Richard B. Stiehl (Chair) and Clait E. Braun; for the WOS Travel Awards, Alexander Wilson Prize, and Lynds Jones Prize—Charles R. Blem (Chair), Leann Blem, Lynn B. Martin, and David Podlesak.

COMMENDATION

WHEREAS the Wilson Ornithological Society and the Association of Field Ornithologists held a joint meeting in Galveston, Texas, at the invitation of the Houston Audubon Society and the Gulf Coast Bird Observatory; and

RECOGNIZING that the Committee on the Scientific Program, under the capable direction of Charlie Blem, provided an outstanding program of oral and poster presentations, including a symposium on the application of radar technology to the study of avian migration; and

RECOGNIZING that the Committee on Local Arrangements, through the efforts of Dwight Peake and other members of the Houston Audubon Society, especially the Galveston County Group of the HAS, provided a conference venue with comfortable accommodations and extraordinary bird watching experiences, in which attendees saw well over 100 species of birds in a single day, and life lists grew inordinately;

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society commend the Committee on the Scientific Program, the Committee on Local Arrangements, and our Texan hosts for a delightful and informative meeting in Galveston.

COMMENDATION

WHEREAS Robert Beason has served the Wilson Ornithological Society as editor of its principal organ, *The Wilson Bulletin,* for the past three years; and

WHEREAS Bob Beason's unflagging efforts have resulted in increases in the efficiency by which the journal is published, the shortening of time from receipt of manuscript to date of decision, and an overall increase in the selectivity of papers accepted for publication; and

WHEREAS *The Wilson Bulletin* continues to be of the highest editorial and scientific quality, exemplary of a leading ornithological journal;

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society extends its sincerest appreciation and thanks to Bob Beason for his efforts on behalf of the society and for a job well done.

Both commendations were enthusiastically passed by acclamation.

Following the award presentations and commendations, the guest speaker, Sidney A. Gauthreaux, Jr., gave a marvelous keynote address on radar studies of bird migration, which was well received.

WOS BUSINESS MEETING

In deviation of tradition, the Wilson Ornithological Society conducted its annual business in one business meeting, rather than two. The single business meeting was called to order by President Kricher at 20:31 on Friday, 27 April, in Music Hall. Secretary Smallwood presented a synopsis of Wednesday's council meeting, noting that as of 21 March 2000, the society's membership stood at 2219 individuals, including 261 students, and that 717 libraries and institutions subscribed to *The Wilson Bulletin.* Secretary Smallwood and Council Member Sara Morris elaborated on two issues regarding the society's role in the new era of information technology. First, the WOS has pledged financial support in response to a proposal from Peter Stettenheim to create a searchable database containing all the citations in *Recent ornithological literature* and *Recent ornithological literature online* since 1983. Second, Council supported, in concept, participation with BioOne, a non-profit corporation formed to publish electronic versions of biological journals. The WOS Publications Committee is studying the proposal.

Next year's meeting will be at the Fayetteville Hilton and University of Arkansas Center for Continuing Education from 3–6 May, 2001, at the invitation of Local Chair Doug James. The 2002 annual meeting will be held in Ft. Meyers, dates to be announced, hosted by the Florida Gulf Coast University Louis, with Jerry Jackson chairing the local committee. Council gratefully accepted the invitations from Local Chair Jed Burtt to host the 2003 annual meeting at Ohio Wesleyan University in Delaware, Ohio, during March, and from Scott Sutcliffe to host the 2004 meeting at Cornell University during late September or early October.

The secretary then asked those assembled to stand in recognition of the following members who had died since we last met: Donald C. Alexander (Winthrop, ME), Robert E. Ball (North Canton, OH), Richard R. Graber (Golconda, IL), Wilma S. Klick (Mitchellville, MD), Robert R. Knickmeyer (Hazelwood, MO), H. Elliot McClure (Camarillo, CA), Henri Ouellet (Hull, PQ), David F. Parmelee (Las Vegas, NV), Mary J. Robertson and William B. Robertson, Jr. (Homestead, FL), Arnold Small (Beverly Hills, CA), Phoebe B. Snetsinger (Webster Groves, MO), A. M. Sorrill (Quincy, IL), Ann T. Tarbell (Bolingbrook, IL), and Morgan C. Webb (Sioux City, IA).

The treasurer's report was then presented by Doris Watt. A motion by Sandy Gaunt, seconded by Susan Smith, to accept the treasurer's proposed budget for 2000/2001 passed unanimously.

President Kricher presented the editor's report for Bob Beason, who was not able to attend, and informed those present that Council had elected John Smallwood to succeed the retiring Editor Beason.

Jerry Jackson, Chair, presented the report of the nominating committee, which also included Mary Clench and Danny Ingold: President, John C. Kricher; First Vice-President, William E. Davis, Jr.; Second Vice-President, Charles R. Blem; Secretary, Sara R. Morris; Treasurer, Doris J. Watt; Members of Council for 2000–2003, Susan M. Smith and W. Herbert Wilson. Having asked for additional nominations from the floor and hearing none, Past President George Hall's suggestion to "turn the rascals out" notwithstanding, President Kricher closed the nominations as a result of a motion by Mary Clench, seconded by Toby Gaunt. Further, Mary Clench moved and Toby Gaunt seconded that the secretary cast a single unanimous vote for the slate of nominees, and by acclamation, it became so. Adjournment occurred at 20:48.

REPORT OF THE TREASURER

1 July 1999 through 1 April 2000

GENERAL FUNDS

Balance Forward		$ 84,508.94
Receipts		
Regular and Sustaining Memberships	$30,860.00	
Student Memberships	$ 3,997.00	
Family Memberships	$ 120.00	
Total Dues		$ 34,977.00
Subscriptions	$25,165.00	
Newsletter	$ 208.00	
Back Issues	$ 337.25	
Page Charges	$ 8,950.00	
Total Income from Publications		$ 34,660.25
Contributions: Research Fund	$ 395.00	
Van Tyne Library	$ 336.00	
General Endowment	$ 113.00	
Life, Patrons (Gen Endowment)	$ 875.00	
Unrestricted	$ 641.00	
Total Contributions		$ 2,360.00
Royalties	$ 382.79	
Interest from Checking Account	$ 464.95	
Interest from Endownments	$31,531.89	
Dividends from Dreyfus Acct (reinvested)	$ 840.22	
Subtotal		$ 33,219.85
Miscellaneous		$ 10.56
Net OSNA Adjustment		–$ 2,146.35
TOTAL RECEIPTS		$ 103,081.31
Disbursements		
Bulletin Publication		
June 1999	$16,369.79	
September 1999	$17,848.52	
December 1999	$18,934.68	
March 2000	$16,094.00	
Editor's expenses	$ 6,187.32	
Total Publication Costs		$ 75,434.31
Flock	$	
OSNA Expenses (98)	$ 5,856.80	
OSNA Expenses (99)	$	
Officer's expenses	$ 250.48	

CPA (tax filing)	$ 475.00	
Incorporation fee	$ 5.00	
Editor's honorarium	$ 2,000.00	
Editor's travel	$ 500.00	
Library	$ 1,000.00	
99 Meeting costs	$ 1,677.70	
2000 Meeting costs so far	$ 329.00	
Miscellaneous	$ 950.22	
Total Operating Expenses		$ 13,044.20
Organizational Awards	$	
Ornithological Council Contribution	$ 2,000.00	
ABC Dues	$	
Total Philanthropies		$ 2,000.00
TOTAL DISBURSEMENTS		$ 90,478.51
Ending Balance		$ 97,111.74

CASH ACCOUNTS

First Source Bank Checking 1 April 2000	$73,609.36	
Dryfus Liquid Assets 1 April 1999	$23,502.38	
Total Cash on Hand		$ 97,111.74
Van Tyne Library Accounts		
Starting Balance	$ 8,274.29	{$7,296}
Receipts	$ 4,365.70	
Expenses	$ 3,070.66	
Ending Balance		$ 9,569.33

SUTTON DESIGNATED ACCOUNT

Endowment Principal as of 1 July 99	$68,961.78	
Incr in Principal Value 99–2000*	$70,961.67	
1999 Earnings*	$ 2,057.87	
Funds disbursed for Color Plates (4)	$ 3,410.00	
Balance		–$ 1,352.13

TOTAL ENDOWMENT FUNDS

1997 Market Value	$ 814,315.00
1998 Market Value	$ 968,838.00
1999 Market Value	$1,096,733.81
2000 Market Value (Mar 31)	$1,097,350.63

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*Based on 2.9% yield on Mellon Account

Doris J. Watt, *Treasurer*

EDITOR'S REPORT—1999

During 1999, the editorial office of *The Wilson Bulletin* received 225 manuscripts, 20 fewer than the previous year. The acceptance rate was 33%, compared to 40% for past years. The review process took an average of 3 months and most manuscripts were returned to the authors with reviewers' comments 2–4 months after receipt. Using e-mail for much of the correspondence with authors and reviewers has resulted in monetary savings from postage and faster turn around for manuscripts; in some cases the author received a decision within a month of submission.

The size of *The Wilson Bulletin* has remained at approximately 600 pages per volume. Three issues in 1999 contained color frontispieces and two of the three issues that are out or in the works for 2000 contain color frontispieces.

I greatly appreciate the assistance of the editorial board (Clait Braun, Richard Conner, and Kathy Beal) for their timely advise on many manuscripts, especially Kathy G. Beal for help with manuscripts having difficult statistical problems and for doing the index. Editorial assistants Tara Baideme, Melanine Daniels, John Lamar, Dante Thomas, and Doris Watt assisted in tracking and checking the many manuscripts. The State University of New York at Geneseo and the Biology Department continue to support the editor and the running of the editorial office in many ways.

Robert C. Beason, *Editor*

The reports of the standing committees are as follows:

REPORT OF THE MEMBERSHIP COMMITTEE

Current members of the WOS membership committee are Laurie Goodrich, Chair, Hawk Mountain (PA), Jim Ingold of Louisiana State University (LA), John

Smallwood of Montclair State University (NJ), Amanda Rodewald of Pennsylvania State University (PA), and Danny Ingold of Muskingum College (OH). Chrissy Howell resigned from the committee due to school commitments.

The membership poster was displayed during the last year at the American Ornithological Union meeting in Ithaca, New York, the Pennsylvania Wildlife Society meeting in Williamsport (PA), March 1999, and the Wilson Society meeting in Maine during May 1999. Brochures were also displayed at a few meetings, including the Raptor Research Foundation meeting in La Paz, Mexico.

During 1999, the chair responded to 20 or more inquiries from people regarding membership issues. Most people seem to be accessing the WOS website to locate membership information. All inquiries were forwarded to Allen Press and the OSNA Director, Anthony Bledsoe, and were handled promptly. OSNA monthly membership updates have been received by the membership chair in recent months. We continue to work with the OSNA Director and Allen Press to improve the exchange of membership information.

Membership Committee Member Jim Ingold sent 11 membership invitation letters to non-members who gave papers at the May 1999 Wilson meeting. He plans to send some letters to the 1998 joint meeting participants as well. Danny Ingold has been working on sending letters to people that did not renew their memberships in 1999. A total of 88 letters were sent with approximately 10% responding. Some positive feedback has been received to this membership inquiry letter.

The membership brochure was revised by John Smallwood with input from Robert Beason, Doris Watt, and others. It will be reprinted shortly. Additional green brochures were located, so printing was delayed in order to use up the old brochures. WOS members are encouraged to display and hand out brochures at meetings, schools, and functions they attend. Contact the membership chair for extra brochures.

A new, modernized WOS membership display is in production. A larger folding tabletop display was purchased during the summer (blue and grey background color) and graphic material was provided by several WOS council members. We hope to have the display finalized for the Texas meeting. This display is larger and will have an optional lighted header. Because it will be larger, we plan to ship the display to and from the meeting sites by UPS in most cases. This will make it easier for people to host the display since it will not have to be carried through an airport. WOS council members are encouraged to adopt the display for a meeting during the coming year. With advance notice, the membership chair will ship the unit to the meeting site. Smaller free-standing, brochure holders may also be produced for portable display opportunities. The committee would like to request that any council member attending a meeting consider helping out with the display. To volunteer, contact Laurie Goodrich by e-mail at goodrich@hawkmountain.org. If unable to put up a display, please take a stack of brochures for distribution tables.

Laurie J. Goodrich, *Chair*

REPORT OF THE UNDERGRADUATE OUTREACH COMMITTEE

At the 1999 meeting in Waterville, Maine, the committee hosted a workshop on bird skin preparation, led by Janet Hinshaw. We continue to maintain the *Guide to Graduate Studies in Ornithology in North America* on the WOS home pages to provide information for undergraduates and post-graduates interested in pursuing a graduate degree in ornithology. Jed Burtt continues his preparation for the dissemination of laboratory exercises presented by a number of participants at our workshop at the Cape May meeting in 1996. We are considering offering a workshop at a future meeting on recording and analyzing bird vocalizations.

W. Herbert Wilson, Jr., *Chair*

REPORT OF THE JOSSELYN VAN TYNE MEMORIAL LIBRARY COMMITTEE

The following happened over the past calendar year with respect to the library loans:

- Loans of library materials to members included 81 transactions to 41 people or institutions. These loans included 48 books, and 244 journals and photocopied articles.

Acquisition of volumes:

- A total of 143 publications were received by exchange from 115 organizations or individuals. 29 journals were gifts from 24 organizations and 30 more were obtained via 25 subscriptions.
- 1356 items were donated by members, friends, and libraries. These donations included 37 books, 481 journal issues, 708 reprints, and 129 reports and miscellaneous items.
- 12 members, friends and libraries donating materials included James Armacost, Clait Braun, J. Buki (for the Hungarian Ornithological Society), Julie Craves, Steve Goodman, Janet Hinshaw, Lloyd Kiff (for The Peregrine Fund), Martin McNicholl, Sara Morris, William Scharf, Jeffrey Spendelow, and Dawn Wilkins.
- New items purchased for $2062.59 included 28 books.

Dispersal of volumes:

- 555 journal issues were given as gifts to five libraries (Walter Thiede, The Peregrine Fund, Point Reyes Bird Observatory, Hungarian Institute of Ornithology, and Whitefish Point Bird Observatory).
- In 1999 we sold 139 books and 18 journal issues for $3608.58 (this includes postage).
- As part of our effort to decrease our stock of back issues of *The Wilson Bulletin,* we sent out 2208 old issues for free (for the cost of postage) to about 55 individuals and libraries.

Accessibility on the Web:

- The website http://www.ummz.lsa.umich.edu/birds/

wos.html continues to be enhanced. Journals currently received are listed on the site as well as how to access the University of Michigan's on-line catalogue, which can be used to check holdings.

- A list of 460 books for sale are on line currently with several hundred to be added soon. We have an on-line ordering ability. Please visit the website soon and check it out!!

Janet Hinshaw hired five people (mostly students) to help her in the library. Their tasks included processing gifts, and boxing and sending out *Wilson Bulletin* back issues and duplicate books. Their wages amounted to about $1270.

We still need to reduce our stock of back issues of *The Wilson Bulletin.* We would like to have help from the Council in identifying libraries, people, and institutions that could benefit from getting back issues.

In closing, I want to offer my thanks to those people who make the JVTML work so efficiently, including Joann Constantinides, the secretary for the Bird Division in the Museum of Zoology, who handles many of the library requests, and of course THE most important person connected with the library, Janet Hinshaw, who literally "runs the show" by making sure the library is kept up-to-date, and as useful to members and friends as possible. Janet makes my job quite easy.

Terry L. Root, *Chair*

The Committee on the Scientific Program, consisting of Charles Blem, Chair, Leann Blem, Lynn B. Martin, and David Podlesak, presented the following program, assisted by session moderators Edward H. Burtt, Jr., Richard N. Conner, Lynn Martin, David Podlesak, and Robert C. Whitmore, and symposium organizers John Black and Daphne Gemmill.

PAPER SESSIONS

F. Amidon, C. Haas, and J. Morton, Virginia Polytechnic Inst. and State Univ.. Blacksburg, VA, "Rota Bridled White-eye foraging habitat selection."

B. W. Baker, T. R. Stanley, J. A. Sedgwick, Midcontinent Ecological Science Center, USGS, Fort Collins, CO, and G. E. Plumb, Yellowstone Center for Resources, Yellowstone National Park, WY, "Is nest predation higher on prairie dog colonies?"

J. C. Barlow and S. Leckie, Royal Ontario Museum, Toronto, ON, "Do Gray Vireos, breeding in southeastern Colorado, winter in Texas?"

W. C. Barrow, Jr., National Wetlands Research Center, USGS, Lafayette, LA, and I. Renne, Clemson Univ., Clemson, SC, "Interactions between migrant landbirds and an invasive exotic plant, the Chinese Tallow Tree."

C. A. Bassett, Southeastern Louisiana Univ., Hammond, LA, "Habitat selection of the Swainson's Warbler."

K. A. Baum, Texas A&M Univ., College Station, TX, "The significance of color cues for hummingbird foraging patterns."

J. Black, Brock Univ., St. Catharines, ON, Canada, "Application of weather radar to monitoring numbers of birds in migration."

C. R. Blem, L. B. Blem, and C. Hyman, Virginia Commonwealth Univ., Richmond, VA, "Demographics of female Prothonotary Warblers in eastern Virginia: effects of changing climate?"

D. W. Brauning and D. Diefenbach, Pennsylvania Game Commission, Harrisonburg, PA, and Pennsylvania Cooperative Fish and Wildlife Research Unit, Pennsylvania State Univ., University Park, PA, "Analysis of distance sampling methodology for grassland bird population studies."

R. P. Brooks, Pennsylvania State Cooperative Wetlands Center, Pennsylvania State Univ., University Park, PA, R. S. Mulvihill, Powdermill Nature Reserve, Carnegie Museum of Natural History, Rector, PA, T. Master, East Stroudsburg Univ., East Stroudsburg, PA, and T. J. O'Connell, Pennsylvania State Cooperative Wetlands Center, Pennsylvania State Univ., University Park, PA, "Breeding biology of Louisiana Waterthrush (*Seiurus motacilla*) in Pennsylvania."

R. A. Canterbury, Concord College, Athens, WV, "Testing evolutionary and ecological hypotheses in a transient hybridization zone using path analysis and structural equation modeling."

R. A. Canterbury, Concord College, Athens, WV, and B. M. Walton. Cleveland State Univ., Cleveland, OH, "Effects of temperature and body mass on metabolism in feral pigeons, *Columba livia.*"

A. N. Chadwick, J. R. Walters, and C. A. Haas. Virginia Polytechnic Inst. and State Univ., Blacksburg, VA, "Within-site selection of artificial cavity trees by Red-cockaded Woodpeckers."

D. Cimprich, Univ. of Southern Mississippi, Hattiesburg, MS, "A function of vocalization during autumn migratory stopover."

C. S. Collins, R. N. Conner, and D. Saenz, Southern Research Station, USFS, Nacogdoches, TX, "The influence of hardwood midstory and pine species on pine bole arthropods: potential implications on Red-cockaded Woodpecker foraging."

R. N. Conner, Southern Research Station, USFS, Nacogdoches, TX, J. R. McCormick, Stephen F. Austin State Univ., Nacogdoches, TX, R. R. Schaefer, and D. Saenz, Southern Research Station, USFS, Nacogdoches, TX, "A Red-cockaded Woodpecker group with two simultaneous nest trees."

S. T. Feirer and D. M. Leslie, Jr., Oklahoma Cooperative Fish and Wildlife Research Unit, Oklahoma State Univ., Stillwater, OK, "Geographical information system in the study of the avian community on Ralstin Island, Oklahoma."

C. Field, Smith College, Northampton, MA, and J. L. Atwood, Antioch New England Graduate School, Keene, NH, "The role of subcolonies in a Least Tern colony in Massachusetts."

E. D. Fink, A. A. Woodward, Univ. of Missouri, Columbia, MO, and F. R. Thompson, III, North Central Research Station, USFS, Columbia, MO, "Habitat use and reproductive success of shrubland songbirds in the Missouri Ozarks."

K. Flaagan, California State Univ., Fullerton, CA, "Nest-site selection of the coastal Cactus Wren *Campylorhynchus brunneicapillus* in Chino Hills State Park, California."

J. L. Ganey, W. M. Block, B. E. Strohmeyer, and J. P. Ward, Jr., Rocky Mountain Research Station, USFS, Flagstaff, AZ, "Home range, habitat use, and vital rates of Mexican Spotted Owls in two different landscapes."

S. L. L. Gaunt, Ohio State Univ., Columbus, OH, and L. F. Baptista, California Academy of Sciences, San Francisco, CA, "Song divergence in two populations of Green-violet Ear Hummingbirds."

C. Gellin and S. R. Morris, Canisius College, Buffalo, NY, "Directional patterns of stopover during spring and fall migration on Appledore Island, Maine."

V. Hake, Univ. of Texas at Arlington, Arlington, TX, "Radio waves from VHF transmitters and the effect on homing ability in *Columbia livia*."

C. R. Hathcock, Univ. of Texas-Pan American, Edinburg, TX, "Impact on host reproduction of the brood-parasitic Bronzed Cowbird (*Molothrus aeneus*) in the lower Rio Grande Valley, Texas."

L. A. Hennings, Oregon State Univ., Corvallis, OR, J. Budhabhatti, Metropolitan Regional Government, Portland, OR, and W. D. Edge, Oregon State Univ., Corvallis, OR, "Do avian communities support Portland Metro's model for ranking habitats for conservation?"

A. Herb, Jr., and D. B. Burt, Stephen F. Austin State Univ., Nacogdoches, TX, "Habitat requirements and cooperative breeding in the Brown-headed Nuthatch."

D. J. Ingold, Muskingum College, New Concord, OH, "The use of a reclaimed strip-mine by grassland nesting birds in east-central Ohio."

A. B. Johnson and E. H. Burtt, Jr., Ohio Wesleyan Univ., Delaware. OH, "Double-scratching behavior of Song and American Tree Sparrows foraging on different substrates."

K. Jungbluth, NWS Forecast Office, Des Moines, IA, "Classic examples of nocturnal migration liftoff using the Des Moines WSR-88D."

S. Kelling, Cornell Laboratory of Ornithology, Ithaca, NY, "National Audubon Society and Cornell Laboratory for Ornithology's Birdcast Pilot Project to use NEXRAD data, with nocturnal vocalization monitoring, and ground truthing: application for bird conservation."

T. A. Kelly, USAF, Valdosta, GA, "The Avian Hazard Advisory System (AHAS): operational use of weather radar for reducing bird strike risk in North America."

M. Khan and J. Walters, Virginia Polytechnic Inst. and State Univ., Blacksburg, VA, "Effects of helpers on breeder survival in the Red-cockaded Woodpecker."

J. C. Kilgo, Southern Research Station, USFS, New Ellenton, SC, "Effect of group selection timber harvest in bottomland hardwoods on prey availability and foraging efficiency of Hooded Warblers."

R. Larkin, Illinois Natural History Survey, Urbana, IL, "Evolution of weather radar use for ornithology."

R. P. Larkin and R. Diehl, Illinois Natural History Survey, Urbana, IL, "Ground truthing the location and bird species composition."

S. Lohr, S. Gauthreaux, Clemson Univ., Clemson, SC, and J. Kilgo, Southern Research Station, USFS, New Ellenton, SC, "The impact of standing and downed coarse woody debris removal on breeding and nonbreeding birds in loblolly pine (*Pinus taeda*) forests."

L. B. Martin, Univ. of Illinois, Urbana, IL, "Woodpecker snag preference in a managed Virginia hardwood forest."

J. R. McCormick, Stephen F. Austin State Univ., Nacogdoches, TX., R. N. Conner, and D. Saenz, Southern Research Station, USFS, Nacogdoches, TX, "Delayed reproduction of reintroduced Red-cockaded Woodpeckers."

R. W. McFarlane, McFarlane & Associates, Houston, TX, "Population trends of gulls, terns and skimmers in Texas."

J. G. Morgan, Houston, TX, "A 21-year compilation of weather related groundings of Neotropical migrant songbirds on the upper Texas Coast."

E. S. Morton, Smithsonian Inst., Front Royal, VA, "Mating system, territorial system, bird song, and latitude."

H. Mueller, D. Berger, N. Mueller, G. Allez, W. Robichaud, and J. Kaspar. Cedar Grove Ornithological Station, Cedar Grove, WI, "The cyclic invasions of Northern Goshawks at Cedar Grove, WI (1951–1999)."

R. Nagarajan, J. D. Goss-Custard, Inst. of Terrestrial Ecology, Furzebrook Research Station, Wareham Dorset, UK, and S. E. G. Lea, School of Psychology, Washington Singer Labs, Univ. of Exeter, Exeter, UK, "How do oystercatchers (*Haematopus ostralegus*) increase their intake rate?"

T. O'Bannon, NWS Operational Support Facility, Norman, OK, "The latest in weather radar technology and the availability of the data and application for ornithologists."

T. O'Bannon, NWS Operational Support Facility, Norman, OK, and R. Larkin, Illinois Natural History Survey, Urbana, IL, "Problems in interpreting base reflectivity: weather, birds, insects, anomalous propagation (panel discussion)."

T. O'Connell and R. Brooks, Pennsylvania State Cooperative Wetlands Center, Pennsylvania State Univ., University Park, PA. "Thresholds of forest extent for breeding birds in the mid-Atlantic highlands."

F. S. Peace, Houston, TX, "Watching Broad-winged Hawks on your home computer."

D. W. Podlesak and C. R. Blem, Virginia Commonwealth Univ., Richmond, VA, "Factors affecting the growth and survival of nestling Prothonotary Warblers in Virginia."

J. D. Rising, Univ. of Toronto, Toronto, ON, Canada, "Geographical variation and systematics of saltmarsh Savannah Sparrows."

D. C. Rudolph and R. N. Conner, Southern Research Station, USFS, Nacogdoches, TX, "Red-cockaded Woodpecker populations: what difference does a decade make?"

D. Saenz, Southern Research Station, USFS, Nacogdoches, TX., K. A. Baum, Texas A&M Univ., College Station, TX, R. N. Conner, and D. C. Rudolph, Southern Research Station, USFS, Nacogdoches, TX, "Reintroduction strategies for Red-cockaded Woodpeckers."

M. E. Schmidt and G. H. Farley, Fort Hays State Univ., Hays, KS, "Hypothesized mortality patterns at a recent tower kill in western Kansas."

M. Schmitz and D. Westmoreland, U.S. Air Force Academy, Colorado Springs, CO, "Effects of egg coloration on heat acquisition from sunlight."

J. A. Sedgwick, Midcontinent Ecological Science Center, USGS, Fort Collins, CO, "Geographic variation in the song of the Willow Flycatcher."

J. M. Semprebon, Antioch New England Graduate School, Keene, NH, and W. H. Barnard, Norwich Univ., Northfield, VT, "Vocal characteristics of Gray Jays in Vermont."

V. Shafer and B. Burt, Stephen F. Austin State Univ., Nacogdoches, TX, "A phylogenetic analysis of cooperative breeding in the class Aves."

R. Stefani, Sierra Nevada Framework Project, USFS, Sacramento, CA, "Spatially-explicit risk assessment of the Willow Flycatcher population in the Sierra Nevada Mountains."

K. L. Tettemer, P. A. McDowell, and E. H. Burtt, Jr., Ohio Wesleyan Univ., Delaware, OH, "Do microbes in abandoned nests deter subsequent use of the nest?"

R. Thill, R. Perry, N. Koerth, Southern Research Station, USFS, Nacogdoches, TX, P. Tappe, and D. Peitz, Univ. of Arkansas, Monticello, AR, "Initial bird responses to alternative pine regeneration methods in Arkansas and Oklahoma."

D. Westmoreland, U.S. Air Force Academy, Colorado Springs, CO, "Is egg pigmentation an adaptation for camouflage?"

R. C. Whitmore, West Virginia Univ., Morgantown WV, and M. M. Whitmore, Morgantown, WV, "Songs of the Mangrove Warbler (*Dendroica petechia castaneiceps*) from Baja California Sur, Mexico: thoughts on divergence in isolated populations."

J. B. Whittier and D. M. Leslie, Jr., Oklahoma Cooperative Fish and Wildlife Research Unit, Oklahoma State Univ., Stillwater, OK, "Anthropogenic impacts on Interior Least Tern at a critical breeding site in Oklahoma."

K. A. Wohlfort and J. L. Atwood, Antioch New England Graduate School, Keene, NH, "Time-activity budgets of non-nesting Common Loons in New Hampshire during the breeding season."

D. M. Woods and C. Caffrey, Oklahoma State Univ., Stillwater, OK, "California Least Tern chick feeding rates and their relationship to fledging success."

POSTERS

J. L. Atwood, C. A. Reynolds, M. R. Fugagli, and A. Pairis, Antioch New England Graduate School, Keene, NH, "California Gnatcatcher distribution and its relation to fire history."

R. C. Banks, USGS, PWRC, USNM, Washington, DC, "The Cuban Martin in Florida."

L. Bhatti, J. Shull, Canisius College, Buffalo, NY, A. R. Clark, Buffalo Museum of Science, Buffalo, NY, and S. R. Morris, Canisius College, Buffalo, NY, "Analysis of television tower mortality of migrant bird species in western New York."

T. A. Carrillo, K. Withers, and J. W. Tunnell, Texas A&M Univ. at Corpus Christi, Corpus Christi, TX, "Shorebird utilization of microhabitats in a south Texas coastal wetland mosaic."

C. Y. Chen and G. H. Farley, Fort Hays State Univ., Hays, KS, "Influences of weather on three decades of mist-net captures."

E. D. Fink, A. A. Woodward, Univ. of Missouri, Columbia, MO, D. E. Burhans, North Central Research Station, USFS, Columbia, MO, J. Demand, Missouri Dept. of Conservation, Columbia, MO, and F. R. Thompson, III, North Central Research Station, USFS, Columbia, MO, "An evaluation of observer variability in four measures of nest concealment."

C. M. Francis, Bird Studies Canada, Port Rowan, ON, Canada, and D. J. T. Hussell, Ministry of Natural Resources, Peterborough, ON, Canada, "The Canadian migration monitoring network: tracking bird population trends in Canada."

J. Long and D. Brown, Southeastern Louisiana Univ., Hammond, LA. The effect of experimental fruit removal on territory structure of winter Hermit Thrushes."

S. M. Murphy and T. J. Mabee, ABR Inc., Forest Grove, OR, "Status of Black Oystercatchers in Prince William Sound 10 years after the Exxon Valdez oil spill."

S. Newland and G. H. Farley, Fort Hays State Univ., Hays, KS, "Descriptions of Gray Catbird and Dickcissel nestling development."

C. Pierce, Antioch New England Graduate School, Keene, NH, "Distribution of Bicknell's Thrush (*Catharus bicknelli*) in the Catskill Mountains of New York."

D. A. Rintoul, Kansas State Univ., Manhattan, KS, "Fatty acid composition of different adipose depots of Lapland Longspurs and Sandhill Cranes."

M. Stake, The Nature Conservancy of Texas, and J. D. Cornelius, Natural Resources Branch, Fort Hood, TX, "Video monitoring of Black-capped Vireo nest predation at Fort Hood, Texas."

R. Tankersley, Jr., Tennessee Valley Authority, Norris, TN, and A. Kelly, Geo-Marine, Inc., Panama City, FL, "Identifying migratory flyways and stopover habitats: a regional assessment of migrant landbird habitats."

M. E. Tolle, J. T. Baccus, Southwest Texas State Univ., San Marcos, TX, and J. D. Cornelius, Natural Resources Branch, Fort Hood, TX, "Aging and sexing criteria for *Dendroica chrysoparia*."

D. W. White and E. D. Kennedy, Albion College, Albion, MI, "A House Wren legend: dummy nests and choosy females."

J. B. Whittier and D. M. Leslie, Jr., Oklahoma Cooperative Fish and Wildlife Research Unit, Oklahoma State Univ., Stillwater, OK, "Pre-fledging survival of Least Tern chicks."

ATTENDANCE

ALASKA: *Barrow,* Frank Willingham.

ARIZONA: *Flagstaff,* Joe Ganey; *Tucson,* Clait E. Braun.

CALIFORNIA: *Sacramento,* Rosemary Stefani; *Seal Beach,* Clay Elliott, Kelli Flaagan.

COLORADO: *Colorado Springs,* Matthew Schmitz, David Westmoreland; *Ft. Collins,* Bruce Baker, Audrey Ryder, Ronald Ryder, James Sedgwick.

CONNECTICUT: *New London,* Robert Askins.

FLORIDA: *Ft. Myers,* Jerome Jackson; *Gainesville,* Mary Clench; *Panama City,* T. Adam Kelly.

ILLINOIS: *Champaign,* Robb Diehl, Ronald Larking; *Urbana,* Lynn Martin, II.

INDIANA: *Notre Dame,* Doris Watt.

IOWA: *Boone,* Carmen Jungbluth, Karl Jungbluth.

KANSAS: *Garden City,* Tom Shane; *Hays,* Constance Chen, Greg Farley, Jim Schmidt, Mary Schmidt, Jamie Timson; *Leavenworth,* John Schukman; *Manhattan,* David Rintoul; *Wichita,* Scott Newland.

LOUISIANA: *Hammond,* C. Audro Bassett, David Brown, Jennifer Long; *Lafayette,* Wylie Barrow, Jr.; *Shreveport,* James L. Ingold.

MAINE: *Bridgeton,* Robert Clark; *Portland,* Ileze Balodis, Charles Duncan.

MARYLAND: *Bethesda,* Ralph Wright.

MASSACHUSETTS: *Amherst,* Don Kroodsma; *Foxboro,* William E. Davis, Jr.; *Manomet,* Hamilton Bowman, Mrs. Hamilton Bowman; *Northampton,* Cathryn Field, Kurt Karwacky; *Norton,* John Kricher; *South Hadley,* Susan Smith.

MICHIGAN: *Albion,* Dale Kennedy, Doug White; *Ann Arbor,* Janet Hinshaw.

MISSISSIPPI: *Hattiesburg,* David Cimprich.

MISSOURI: *Columbia,* Alix Fink.

NEW HAMPSHIRE: *Hancock,* Kathy Wohlfort; *Keene,* Jon Atwood.

NEW JERSEY: *Cape May,* Tom Parsons; *Hopewell,* Hannah Suthers; *Trenton,* Mary Doscher; *Upper Montclair,* John Smallwood.

NEW MEXICO: *Albuquerque,* Curt Burney.

NEW YORK: *Buffalo,* Arthur Clark, Mary E. Clark, Caren Gellin; *Holley,* David Bonter; *Ithaca,* Steve Kelling, Scott Sutcliffe; *Trumansburg,* Robert Meade; *Williamsville,* Sara Morris.

NORTH CAROLINA: *Chapel Hill,* Helmut Mueller, Nancy Mueller; *Greensboro,* Herb Hendrickson.

OHIO: *Columbus,* Abbot Gaunt, Sandra Gaunt; *Delaware,* Sarah Brennan, Edward H. Burtt, Jr., Andy Johnson, Kristen Tettemer; *New Concord,* Paul Gledhill, Danny Ingold, Amanda L. Murray.

OKLAHOMA: *Oklahoma City,* Timothy D. O'Bannon; *Stillwater,* Shane Feirer, Joanna Whittlier, Denise Woods.

OREGON: *Aloha,* Lori Hennings; *Forest Grove,* Todd Mabee.

PENNSYLVANIA: *Montgomery,* Daniel Brauning, Marcia Brauning; *Pittsburgh,* Ellen Parkes, Kenneth Parkes; *University Park,* Tim O'Connell.

SOUTH CAROLINA: *Clemson,* Jonathan Ariail, Caroll Belser, Andrew Farnsworth, Sidney Gauthreaux; *Columbia,* Steve Lohr, Edmund Taylor, Edmund Taylor, Jr.; *New Ellerton,* John Kilgo.

TENNESSEE: *Norris,* Roger Tankersley.

TEXAS: *Abilene,* Vaniai Arroyo; *Austin,* John Arvin, Clifford Shackleford; *Bellaire,* David Marrack; *Cedar Creek,* Sandra Skrei; *College Station,* Kristen Baum, Karl Schulze; *Corpus Christi,* Robert Benson; *DeSoto,* Valerie Hake; *Edinburg,* Christopher Hathcock; *Friendswood,* Winnie Burkett; *Ft. Hood,* John Cornelius; *Galveston,* Mary Hannigan, Andrea Norfleet, Alice Anne O'Donell, Richard Peake, Mrs. Richard Peake, Mary Thomas; *Houston,* Peggy Boston, Dan Brooks, Jon Hester, Miner Long, Nancy Loomis, Robert McFarlane, James Morgan, Frank Peace, Marion Peace, Scot Sandefur, Natasha Schischakin, Lee Schoen, Don Verser; *Lake Jackson,* Ian Hartzler, Cecilia Riley; *Lufkin,* Tamara Thompson; *Nacogdoches,* D. Brent Burt, Chris Collins, Richard Conner, Priscilla Coulter, Jim McCormick, Craig Rudolph, Daniel Saenz, Valerie Shafer; *San Marcos,* Maria Elena Tolle; *Sugar Land,* Michael Gray; *The Woodlands,* James Stewart.

VERMONT: *Dorset,* Betty Gilbert; *Montpelier,* Jean Sempreton; *Underhill,* Cheryl Pierce.

VIRGINIA: *Alexandria,* Betty Ann Schreiber; *Annandale,* William Clark; *Blacksburg,* Frederick Amidon, Nicole Chadwick, Jeff Walters; *Charlottesville,* Janice Zimmerman, John Zimmerman; *Front Royal,* Gene Morton; *Richmond,* Charles Blem, Leann Blem, David Podlesak; *The Plains,* Christopher Eberly.

WASHINGTON: *Bainbridge Island,* Lee Robinson.

WASHINGTON DC: Richard Banks, Daphne Gemmill.

WEST VIRGINIA: *Athens,* Ronald Canterberry, Mrs. Ronald Canterberry; *Morgantown,* George Hall, Robert Whitmore.

CANADA: *Kanata Ontario,* Erica Dunn, David Hussell; *St. Catharines Ontario,* John Black; *Toronto Ontario,* Jon Barlow, Sheridan Leckie, Jim Rising.

ENGLAND: *Devon,* R. Nagarajan.

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Acknowledgments

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By Kathleen G. Beal

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