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FRONTISPIECE. Five species (Least Flycatcher, *Empidonax minimus*; Veery, *Catharus fuscescens*; Wood Thrush *Hylocichla mustelina*; Common Yellowthroat, *Geothlypis trichas*; and Scarlet Tanager, *Piranga olivacea*) showing significant declines, 1970-2001, in spring and/or fall capture rates at Manomet Center for Conservation Sciences, Massachusetts, and which also showed declining population trends in at least one of three Breeding Bird Survey physiographic strata (southern New England, northern New England, and eastern Spruce-Hardwoods) that were considered likely sources of the migrants passing through Manomet. Painting by Dale Crawford.

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32 YEARS OF CHANGES IN PASSERINE NUMBERS DURING SPRING AND FALL MIGRATIONS IN COASTAL MASSACHUSETTS

TREVOR L. LLOYD-EVANS^{1,3} AND JONATHAN L. ATWOOD^{1,2}

ABSTRACT.—Using standardized mist-net captures collected over a 32-year period (1970–2001), we examined changes in the capture rates of passerines recorded in coastal Massachusetts during fall (78 species) and spring (72 species) migration. Capture rates of 45 species of fall migrants (58%) declined significantly between early (1970–1985) and late (1986–2001) years of the study; 36 species of spring migrants (50%) showed significant declines. Only Carolina Wren (*Thryothorus ludovicianus*), Tufted Titmouse (*Baeolophus bicolor*), Northern Cardinal (*Cardinalis cardinalis*), and Orchard Oriole (*Icterus spurius*) showed significant increases during spring migration; fall sampling indicated that Carolina Wren, Tufted Titmouse, Black-throated Blue Warbler (*Dendroica caerulescens*), and Northern Cardinal had significantly higher capture rates. Of 37 species included in the migration monitoring data but not reliably represented by Breeding Bird Survey (BBS) data in any of the northeastern physiographic strata, 23 (62%) showed significant declines at Manomet during at least one of the two migration periods. There were significant correlations in percent changes in migrant capture rates between fall and spring. BBS trends reported from the southern New England and northern New England physiographic strata were correlated with changes in migrant capture rates. However, there were also inconsistencies between results obtained by the two monitoring approaches, suggesting that factors in addition to actual changes in breeding populations may be reflected in the migration capture data. Received 8 July 2003, accepted 26 March 2004.

Monitoring passerine population changes through counts collected along migratory routes has been attempted often (Hussell 1981, Gauthreaux 1992, Hagan et al. 1992, Hussell et al. 1992, Peach et al. 1998, Ballard et al. 2003) despite a variety of issues that sometimes make the results of such studies difficult to interpret. In particular, detecting true changes in breeding populations may be confounded by weather effects that produce

dramatic differences among years in the numbers of a particular species that appears during migration at a specific site (Gauthreaux 1971, Moore and Simons 1992, Dunn and Hussell 1995); while “fallouts” may provide exciting birding conditions, they also underscore the substantial stochastic element associated with any migration monitoring scheme. Habitat changes at a migration site also may cause apparent shifts in species’ abundances that are unrelated to true population levels (Remsen and Good 1996). Furthermore, the specific breeding populations actually represented by samples of migrants are almost always unknown (Dunn and Hussell 1995), and conceivably may vary from year-to-year at a particular migration site under the influence of differing weather conditions. Thus, there is lit-

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tle doubt, as some have pointed out (Butcher et al. 1993, Sauer 1993, Remsen and Good 1996), that monitoring changes in breeding populations through counts of migrants obtained by mist-net captures is risky business.

Still, most long-term field observers will quickly counter that *something* is happening to the numbers of migrating land birds in eastern North America (Robbins et al. 1989, Terborgh 1989, Askins et al. 1990), and that these perceived changes are not easily discounted simply by the effects of weather variations or local habitat change. In fact, although short-term fluctuations in numbers of migrants recorded at a site may be completely meaningless, we contend that studies of longer duration—despite their inherent complications—may yet help to elucidate true population changes simply by virtue of their long-term perspective.

In this paper we present results, to date, of one of North America's longest migration monitoring efforts, conducted at Manomet Center for Conservation Sciences (formerly Manomet Bird Observatory, MBO) from the late 1960s to the present. A preliminary analysis of some of these data was presented by Hagan et al. (1992); herein, we extend the scope of this earlier work in terms of years, seasons, and species included. For 78 species in fall and 72 species in spring we examine, for the 32-year period 1970–2001, (a) changes in the numbers of individuals captured at Manomet's banding station in coastal Massachusetts, and (b) similarities in patterns of annual fluctuations of capture rates among species. We also compare changes in capture rates with estimates of population trends obtained through a very different type of monitoring study, the North American Breeding Bird Survey (BBS), which also has operated over this extensive time period (Robbins et al. 1986, Sauer 1993, Sauer et al. 2001).

METHODS

Manomet Center for Conservation Sciences, located on the western side of Cape Cod Bay, Plymouth County, Massachusetts (41° 50' N, 70° 30' W), is characterized by brushy, second-growth deciduous woodland, bordered on the east and south by a steep, eroding coastal bluff and on the west and north by brushy wetlands. Dominant tree species on the

7-ha plot include black cherry (*Prunus serotina*), shadbush (*Amelanchier* sp.), red maple (*Acer rubrum*), white oak (*Quercus alba*), and pitch pine (*Pinus rigida*). Common catbrier (*Smilax rotundifolia*), bayberry (*Myrica pensylvanica*), staghorn sumac (*Rhus typhina*), honeysuckle (*Lonicera morrowi*), arrowwood (*Viburnum recognitum*), and poison ivy (*Toxicodendron radicans*) are principal understory species.

Habitat succession was, for the most part, unchecked during the study period, but the site's location on an exposed coastal bluff resulted in annual natural "pruning" by harsh winter storms that probably reduced the degree of change in habitat structure over time. Small fields and grassland borders within the study site are mowed routinely. Historic photos of the area indicate that during the early 1920s most of the study area consisted of open sheep pastures, but by the time banding operations were begun in 1966 the site had already acquired the brushy, second-growth condition that characterizes it today. An individual black cherry tree was photographed in 1966, with a bander for height comparison, in a net lane about 10 m inland from the ocean bluff. By 2003, the tree had grown an estimated 25% in height, probably typical for the exposed coastal net lanes.

From 45 to 50 nylon mist nets (12 m long, 2.6 m high, 4 panels, 36 mm extended mesh) were operated annually from 1970 to 2001, inclusive; because of less complete coverage and imprecise records regarding capture effort expended during the first 4 years of the observatory's existence (1966–1969), we excluded these years from analysis. Nets were kept at fixed locations throughout the study. Opening and closing times of nets were recorded and used for calculating daily capture effort (Robbins 1968); except for closures during adverse weather conditions, generally nets were operated from 0.5 hr prior to sunrise to 0.5 hr after sunset. Thus, 50 nets open for 12 hr equals 600 net hr. Sampling was conducted 5–7 days per week during spring (15 April–15 June) and fall (15 August–15 November) migration.

During the study period, 205,454 individuals of 159 species were banded. Records used in this analysis were selected from the overall database using criteria described be-

low. Only passerines are considered here; scientific names and abbreviation codes for species referenced in the text are provided in the Appendix. Willow and Alder flycatchers were combined, as were Bicknell's and Gray-cheeked thrushes. Palm Warbler races were treated separately as "Yellow" and "Western" Palm warblers. Captures of hybrid "Brewster's" ($n = 3$) and "Lawrence's" ($n = 2$) warblers were counted as Blue-winged Warblers. Repeat captures were eliminated. Locally breeding birds, identified on the basis of well-developed brood patches or cloacal protuberances, were eliminated, as were spring captures of hatching-year (HY) individuals. Species that were captured, by season, in fewer than 15 of the 32 years, were eliminated.

For each species, by season, migration windows were calculated as falling between the 1st and 99th percentiles of all capture dates across all years; any records outside these windows were excluded. These cutoff values are provided in the Appendix. For example, during fall migration, 98% of all captures of American Redstarts occurred from 17 August to 12 October. Any banding activity that took place within this window was considered to represent a legitimate sampling day for this species; days that yielded no redstart captures, but on which nets were open, contributed a value of zero to the overall calculation of capture rate. Any redstart captures that occurred before 17 August or after 12 October were excluded.

For each species (by year and season), we calculated a mean capture rate weighted by the number of hours of mist netting that occurred on each contributing date. That is, in calculating mean seasonal and annual capture rates for a species, the rate obtained on a day when nets were open for 400 net hr was given more emphasis than a rate obtained on a day when only 10 net hr of sampling took place. We used Wilcoxon 2-sample tests to examine long-term trends by testing (for each species, by season) the hypothesis that mean capture rates were equal between Early (1970–1985) and Late (1986–2001) years of the study.

Spearman rank correlations were used to assess concordance between each species' fall and spring capture rates, and between the percent change in mean capture rates (Early ver-

sus Late) for each species and the population trends provided by BBS data (Sauer et al. 2001). These authors commendably cautioned that "Small sample sizes, low relative abundance on survey routes, imprecise trends, and missing data all can compromise BBS results. Often, users do not take these problems into account when viewing BBS results, and use the results inappropriately." When we refer to BBS trends in this paper, we conservatively include only instances where the BBS "Regional Credibility Measure" was in the best-sampled, "blue" category. That is, BBS trends considered by Sauer et al. (2001) to include "important deficiencies" (red) and "deficiencies" (yellow) were not used in the correlation analyses.

Presentation of graphs showing changes in capture rates for each species and season combination in this study would require 150 individual figures. Although obviously beyond the space limitations of this publication, these results are provided online at www.manomet.org. Here, in order to visually summarize major patterns of variation within this large set of data, we calculated 3-year moving averages based on annual mean capture rates, then standardized each of these values as a percent of the maximum rate encountered for each species among all years (by season). Next, we used Ward's minimum variance clustering approach, as implemented by JMP statistical software (SAS Institute, Inc. 2001), to identify, for each season, an arbitrary six groups of species that exhibited similar year-to-year fluctuations in capture rates. Finally, we plotted means and standard errors, calculated from the moving averages for species belonging to each of these clusters.

RESULTS

Of 72 species captured during spring migration, 60 (83%) had lower mean capture rates during 1986–2001 than during 1970–1985 (Table 1). These declines were significant ($P < 0.05$) in 36 species. Twelve species showed higher capture rates during 1986–2001 than during 1970–1985; in four of these (Carolina Wren, Tufted Titmouse, Northern Cardinal, and Orchard Oriole), the increases from Early to Late sampling periods were significant ($P < 0.01$).

During fall migration, 69 of 78 species

TABLE 1. Mean capture rates and percent change between Early (1970–1985) and Late (1986–2001) sampling periods during spring and fall migrations. Population trend data from Breeding Bird Survey (BBS) presented for comparison.

Species	Spring capture rate ^a			Fall capture rate ^a			BBS ^b		
	Early	Late	(% change)	Early	Late	(% change)	SH	nNE	sNE
Eastern Wood-Pewee	0.766	0.464	(-39)	0.183	0.141	(-23)	D	D	d
Yellow-bellied Flycatcher	1.539	1.336	(-13)	0.455	0.297	(-35)*	[i]	I	
Acadian Flycatcher	0.234	0.206	(-12)						[d]
Willow/Alder Flycatcher	3.269	3.730	(14)	0.754	0.557	(-26)	[i]	I	[I]
Least Flycatcher	0.844	0.674	(-20)	0.866	0.328	(-62)**	D	D	D
Eastern Phoebe	0.210	0.200	(-5)	0.531	0.574	(8)	[I]	[i]	[i]
Great Crested Flycatcher	0.535	0.813	(52)				D	I	D
Eastern Kingbird	0.342	0.280	(-18)	0.477	0.108	(-77)*	D	d	D
White-eyed Vireo	0.360	0.155	(-57)**	0.143	0.092	(-36)			[I]
Blue-headed Vireo	0.313	0.265	(-15)	0.461	0.610	(32)	I	I	[i]
Warbling Vireo				0.131	0.074	(-44)	[i]	I	i
Philadelphia Vireo				0.379	0.208	(-45)**	[i]	[i]	
Red-eyed Vireo	1.316	0.783	(-40)*	4.317	2.834	(-34)*	I	[d]	[d]
Blue Jay	7.071	2.767	(-61)**	2.326	1.289	(-45)*	[i]	i	D
Black-capped Chickadee	3.176	0.773	(-76)	37.479	18.411	(-51)	I	I	i
Tufted Titmouse	0.162	0.593	(266)**	3.672	6.520	(78)*	[i]	[I]	[I]
Red-breasted Nuthatch				0.291	0.092	(-68)	I	I	[i]
White-breasted Nuthatch				0.156	0.204	(31)	[i]	I	i
Brown Creeper	0.471	0.148	(-69)**	2.750	1.320	(-52)***	[i]	[i]	[d]
Carolina Wren	0.043	0.146	(240)***	0.072	0.546	(658)***			[I]
House Wren	0.368	0.166	(-55)*	0.269	0.182	(-32)	[d]	[D]	[D]
Winter Wren				0.325	0.224	(-31)	[I]	[i]	[i]
Golden-crowned Kinglet	0.454	0.943	(108)	5.176	3.981	(-23)	I	[i]	
Ruby-crowned Kinglet	4.793	3.014	(-37)	2.964	1.917	(-35)	D	[i]	
Blue-gray Gnatcatcher	0.724	0.385	(-47)**	0.344	0.255	(-26)		[I]	[I]
Veery	1.617	0.722	(-55)**	0.909	0.534	(-41)*	[D]	D	d
Gray-cheeked/Bicknell's Thrush	0.415	0.140	(-66)**	0.342	0.190	(-44)**			
Swainson's Thrush	4.708	2.069	(-56)**	2.181	0.996	(-54)**	[D]	[d]	
Hermit Thrush	3.545	3.706	(5)	3.022	2.548	(-16)	[I]	[i]	[d]
Wood Thrush	1.211	0.398	(-67)***	0.306	0.113	(-63)***	D	[D]	D
American Robin	0.767	0.420	(-45)**	7.925	3.382	(-57)**	i	[d]	d
Gray Catbird	32.243	23.340	(-28)**	24.028	17.410	(-28)**	[D]	D	I
Northern Mockingbird	0.176	0.203	(15)	0.671	0.327	(-51)*	[I]	[I]	[I]
Brown Thrasher	0.893	0.364	(-59)***	0.400	0.111	(-72)***	[D]	[D]	D
Cedar Waxwing	0.499	0.882	(77)	0.474	0.314	(-34)	i	I	I
Blue-winged Warbler				0.228	0.234	(3)		[d]	D
Tennessee Warbler	0.938	0.048	(-95)***	0.381	0.069	(-82)***	[i]	[d]	
Orange-crowned Warbler				0.244	0.157	(-36)	[d]		

TABLE 1. Continued.

Species	Spring capture rate ^a			Fall capture rate ^a			BBS ^b		
	Early	Late	(% change)	Early	Late	(% change)	SH	nNE	sNE
Nashville Warbler	0.304	0.122	(-60)*	0.666	0.428	(-36)*	i	[d]	[d]
Northern Parula	0.555	0.287	(-48)**	0.116	0.050	(-57)*	[I]	[i]	[i]
Yellow Warbler	1.574	1.162	(-26)*	0.528	0.168	(-68)**	[i]	d	[I]
Chestnut-sided Warbler	0.292	0.171	(-41)	0.162	0.126	(-22)	d	[D]	d
Magnolia Warbler	5.105	5.572	(9)	0.998	0.881	(-12)	I	d	[i]
Cape May Warbler				1.087	0.077	(-93)**	[i]	[i]	
Black-throated Blue Warbler	0.910	0.861	(-5)	0.549	0.781	(42)*	[i]	i	[i]
Yellow-rumped (Myrtle) Warbler	1.285	0.965	(-25)	45.991	17.639	(-62)**	I	I	[I]
Black-throated Green Warbler	0.208	0.098	(-53)*	0.325	0.250	(-23)	[nc]	i	[I]
Blackburnian Warbler	0.155	0.090	(-42)*	0.093	0.028	(-70)**	i	[d]	[d]
Prairie Warbler	0.318	0.235	(-26)	0.249	0.187	(-25)		[i]	[D]
Palm Warbler (western)				0.543	0.132	(-76)**			
Palm Warbler (yellow)	0.706	0.900	(28)				[I]		
Bay-breasted Warbler	0.338	0.121	(-64)	1.822	0.254	(-86)**	[D]	[i]	
Blackpoll Warbler	2.881	1.384	(-52)**	14.753	4.268	(-71)**	[d]	[i]	
Black-and-White Warbler	5.244	3.310	(-37)**	1.643	0.802	(-51)**	i	d	d
American Redstart	7.394	4.777	(-35)**	6.351	2.889	(-55)**	d	d	[I]
Ovenbird	2.991	2.057	(-31)*	0.726	0.586	(-19)	[nc]	I	nc
Northern Waterthrush	3.424	2.091	(-39)	1.341	0.654	(-51)**	[d]	[nc]	[nc]
Connecticut Warbler				0.232	0.151	(-35)	[d]		
Mourning Warbler	1.688	1.531	(-9)	0.447	0.244	(-45)**	[d]	[d]	
Common Yellowthroat	9.441	6.769	(-28)*	2.294	1.287	(-44)**	d	D	D
Wilson's Warbler	2.733	1.310	(-52)**	1.150	0.735	(-36)**	[i]		
Canada Warbler	4.548	2.378	(-48)**	0.925	0.596	(-36)*	d	d	[d]
Yellow-breasted Chat				1.334	0.645	(-52)**			[D]
Scarlet Tanager				0.418	0.108	(-74)**	[d]	D	[d]
Eastern Towhee	3.453	1.148	(-67)**	1.135	0.264	(-77)**	[D]	D	D
American Tree Sparrow				0.448	0.140	(-69)**			
Chipping Sparrow	0.165	0.076	(-54)				[d]	[I]	[I]
Field Sparrow	0.144	0.030	(-79)**	0.478	0.104	(-78)**	[d]	D	D
Savannah Sparrow	0.314	0.096	(-70)**				[D]	[i]	[D]
Fox Sparrow				0.181	0.073	(-60)*	[d]		
Song Sparrow	1.174	0.589	(-50)*	2.829	1.952	(-31)*	[D]	[D]	D
Lincoln's Sparrow	0.744	0.418	(-44)	0.314	0.208	(-34)	[i]		
Swamp Sparrow	2.624	1.349	(-49)	1.476	1.447	(-2)	i	i	[i]
White-throated Sparrow	17.076	14.091	(-17)	13.389	7.580	(-43)**	D	D	[D]
White-crowned Sparrow	0.194	0.098	(-50)	0.337	0.145	(-57)*			
Dark-eyed (Slate-colored) Junco	0.915	0.379	(-59)**	4.126	1.474	(-64)**	D	d	[d]

TABLE 1. Continued.

Species	Spring capture rate ^a			Fall capture rate ^a			BBS ^b		
	Early	Late	(% change)	Early	Late	(% change)	SH	nNE	sNE
Northern Cardinal	0.285	0.764	(168)***	0.615	1.444	(135)***	[I]	I	[I]
Rose-breasted Grosbeak	0.199	0.046	(-77)*	0.101	0.034	(-66)**	[D]	[i]	[D]
Indigo Bunting	0.125	0.048	(-61)*	0.076	0.056	(-26)	i	d	D
Red-winged Blackbird	1.219	0.641	(-47)**				[D]	[d]	D
Common Grackle	1.412	1.044	(-26)				d	D	D
Brown-headed Cowbird	0.634	0.259	(-59)**				[D]	D	d
Orchard Oriole	0.170	0.502	(194)**						[d]
Baltimore Oriole	2.671	1.247	(-53)**	1.100	0.676	(-39)*	[D]	[i]	[D]
Purple Finch				1.213	0.168	(-86)***	D	D	[D]
House Finch	0.136	0.116	(-15)	0.375	0.249	(-34)	[I]	[I]	[I]
American Gold- finch	1.175	0.953	(-19)	0.233	0.390	(67)	[d]	[i]	[i]

^a Based on weighted means of capture rates, by year and season ($n = 16$ in both Early and Late periods). % Change = $(\text{Late} - \text{Early})/\text{Early} \times 100$. Significant differences between mean Early and Late capture rates (Wilcoxon 2-sample test) indicated by asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

^b Based on Sauer et al. (2001) analysis of 1966–2000 BBS data from physiographic strata 28 (SH, eastern Spruce-Hardwoods), 27 (nNE, northern New England), and 12 (sNE, southern New England). D = significant ($P < 0.05$) decline; d = non-significant ($P \geq 0.05$) decline; I = significant increase; i = non-significant increase; nc = no change. Symbols in brackets [] indicate that Sauer et al. (2001) considered these trend estimates unreliable due to “deficiencies” or “important deficiencies” in sampling. Blanks indicate physiographic regions where a given species was not represented in BBS trend data.

(88%) had lower capture rates during Late years of the study than during Early years (Table 1); these differences were significant ($P < 0.05$) in 45 species. Nine species had higher capture rates during 1986–2001 than during

1970–1985; in four of these (Carolina Wren, Tufted Titmouse, Black-throated Blue Warbler, and Northern Cardinal), the differences were significant ($P < 0.05$).

Percent changes in mean capture rates from Early to Late years of the study were positively correlated between spring and fall migrations ($Rho = 0.55$, $P < 0.001$, $n = 63$ species; Fig. 1). Exclusion of three outliers (Carolina Wren, Tufted Titmouse, and Northern Cardinal) that showed dramatic increases in capture rates during both migration periods did not substantially alter the strength of the observed correlation ($Rho = 0.48$, $P < 0.001$, $n = 60$ species). There were no species that showed significant increases in capture rate during one season and significant decreases in the other.

Because of uncertainty regarding the location of breeding populations represented by migrants in coastal Massachusetts, we compared our results with BBS trends from three physiographic regions (southern New England, northern New England, and eastern Spruce-Hardwoods) that we considered the most likely sources of the majority of migrants observed at Manomet (Fig. 2). Captures of spring migrants were significantly ($P <$

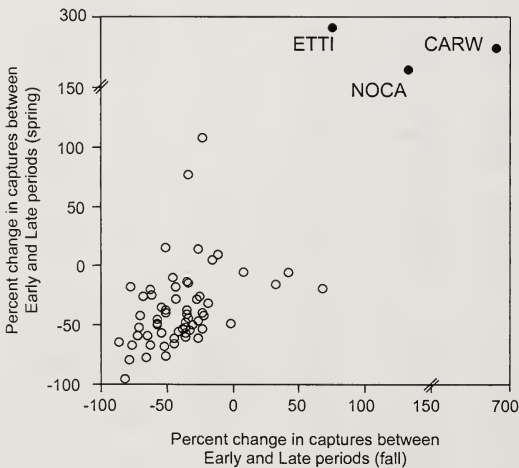


FIG. 1. Correlations between spring and fall migration periods for percent change in capture rates between Early and Late periods of the study ($P < 0.001$, $n = 63$ species). Three apparent outliers (CARW, Carolina Wren; ETTI, Tufted Titmouse; and NOCA, Northern Cardinal) shown as solid circles.

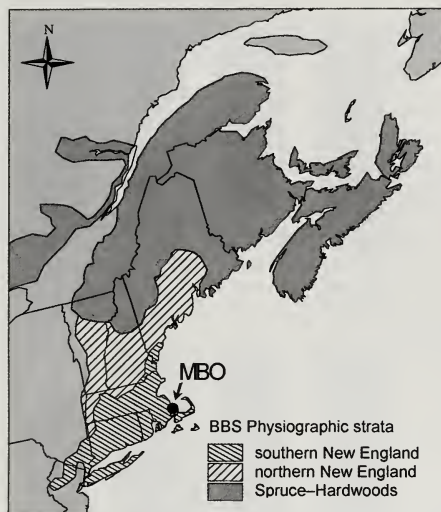


FIG. 2. Location of Manomet Center for Conservation Sciences (MBO) study site relative to three northeastern physiographic strata used in analysis of Breeding Bird Survey data.

0.05) and positively correlated with BBS trends from northern New England; during fall migration, we found significant positive correlations between capture rates and BBS trends from both southern and northern New England physiographic strata (Table 2).

Four species that breed at high latitudes or high elevations [Gray-cheeked/Bicknell's Thrush, Palm Warbler (western), American Tree Sparrow, and White-crowned Sparrow] were represented in the migration monitoring data but not by BBS analyses; all of these species showed significantly declining capture rates ($P < 0.05$) between Early and Late periods of the study. Thirty-three species represented in the migration monitoring data were considered by Sauer et al. (2001) to be represented unreliably by BBS data in any of the northeastern physiographic strata (Table 1); 19 of these species (Philadelphia Vireo, Brown Creeper, House Wren, Blue-gray Gnatcatcher, Swainson's Thrush, Northern Mockingbird, Tennessee Warbler, Northern Parula, Cape May Warbler, Bay-breasted Warbler, Black-poll Warbler, Northern Waterthrush, Mourning Warbler, Wilson's Warbler, Yellow-breasted Chat, Savannah Sparrow, Fox Sparrow, Rose-breasted Grosbeak, and Baltimore Oriole) showed significant declines at Manomet during at least one of the two migration periods,

TABLE 2. Correlations between percent change in mean capture rates (Early versus Late sampling periods) and Breeding Bird Survey trends (Sauer et al. 2001) from three physiographic regions. BBS results with "deficiencies" or "important deficiencies" have been excluded from analysis (see text).

	Physiographic region ^a		
	sNE	nNE	SH
Spring	0.36 (0.087) ^b <i>n</i> = 23	0.45 (0.011) <i>n</i> = 31	0.17 (0.402) <i>n</i> = 26
Fall	0.50 (0.018) <i>n</i> = 22	0.47 (0.006) <i>n</i> = 33	0.34 (0.087) <i>n</i> = 26

^a sNE = southern New England, nNE = northern New England, SH = eastern Spruce-Hardwoods.

^b Spearman rank correlation (P -value).

while capture rates of 3 (Tufted Titmouse, Carolina Wren, and Orchard Oriole) significantly increased during fall and spring migrations (Table 1).

Apparent inconsistencies between trends based on migration captures at Manomet and BBS data were greatest for the eastern Spruce-Hardwoods stratum and least for the southern New England stratum. This pattern was true during both spring (Fig. 3) and fall (Fig. 4) migration periods. Spring migration captures indicated significant ($P < 0.05$) declines in three species for which BBS analyses found significant increases: Red-eyed Vireo (eastern Spruce-Hardwoods), Ovenbird (northern New England), and Gray Catbird (southern New England). Fall migration captures significantly declined in four species whereas BBS analyses showed significant increases: Red-eyed Vireo and Yellow-rumped (Myrtle) Warbler (eastern Spruce-Hardwoods), Yellow-bellied Flycatcher and Yellow-rumped (Myrtle) Warbler (northern New England), and Gray Catbird (southern New England).

For each migration period, cluster analysis was used to identify an arbitrary six groups of species that shared general patterns of change in capture rates across years (Figs. 5 and 6). This approach allowed us to summarize trend data visually for a large number of species. However, we note that similarities in capture rates among members of a group do not necessarily mean that shared trends were caused by similar proximate factors. In some cases cluster membership may, in fact, reflect the influence of shared ecology. For example,

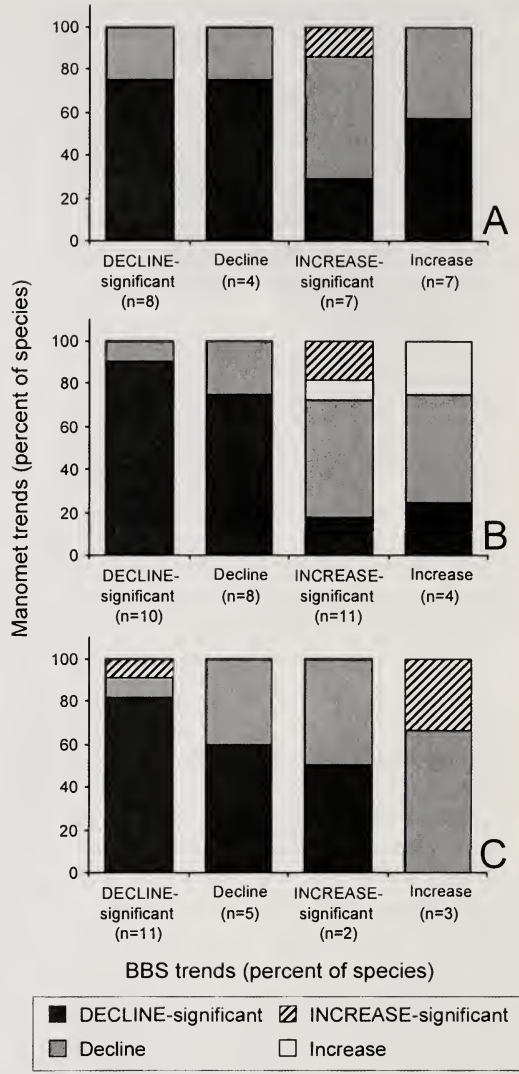
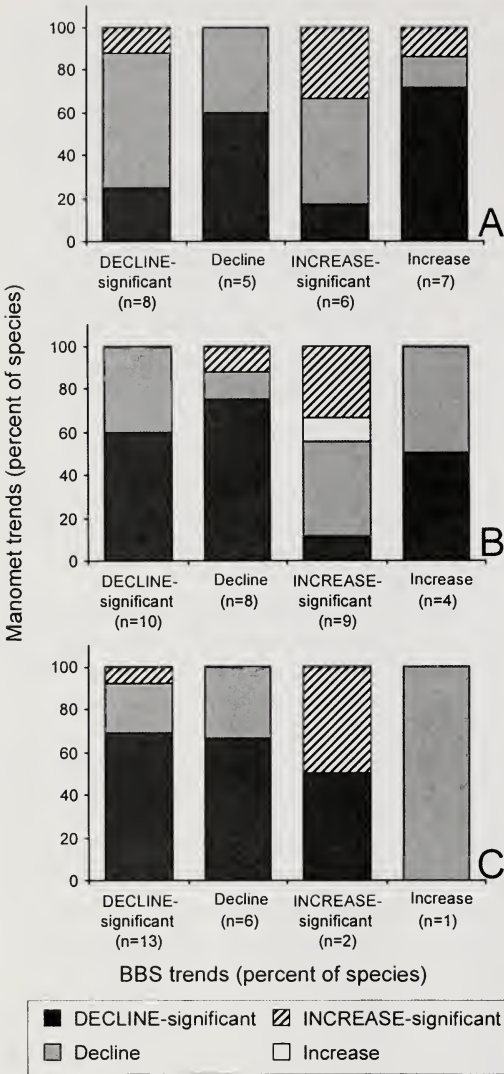


FIG. 3. Comparison of trends in capture rate based on spring migration monitoring at Manomet relative to trends derived from BBS data (Sauer et al. 2001) in (A) spruce-hardwoods, (B) northern New England, and (C) southern New England physiographic strata. "DECLINE-significant," $P < 0.05$; "Decline," $P \geq 0.05$; "INCREASE-significant," $P < 0.05$; "Increase," $P \geq 0.05$. For example, of 13 species showing significant declines according to BBS data from southern New England, 70% showed significant declines in Manomet capture rates, and 20% showed declines in Manomet capture rates that were not statistically significant.

capture rates of Blackpoll Warbler, Northern Parula, Tennessee Warbler, Cape May Warbler, Blackburnian Warbler, and Bay-breasted Warbler peaked during the mid to late 1970s

FIG. 4. Comparison of trends in capture rate based on fall migration monitoring at Manomet relative to trends derived from BBS data (Sauer et al. 2001) in (A) spruce-hardwoods, (B) northern New England, and (C) southern New England physiographic strata. "DECLINE-significant," $P < 0.05$; "Decline," $P \geq 0.05$; "INCREASE-significant," $P < 0.05$; "Increase," $P \geq 0.05$.

(Fig. 6F); many, if not all, of these species likely responded to a widespread outbreak of spruce budworm (*Choristoneura fumiferana* Clem.) in eastern North America during this time period (Hagan et al. 1992). Carolina Wren and Northern Cardinal, two species known to have shown dramatic regional population increases during the last decades (Ha-

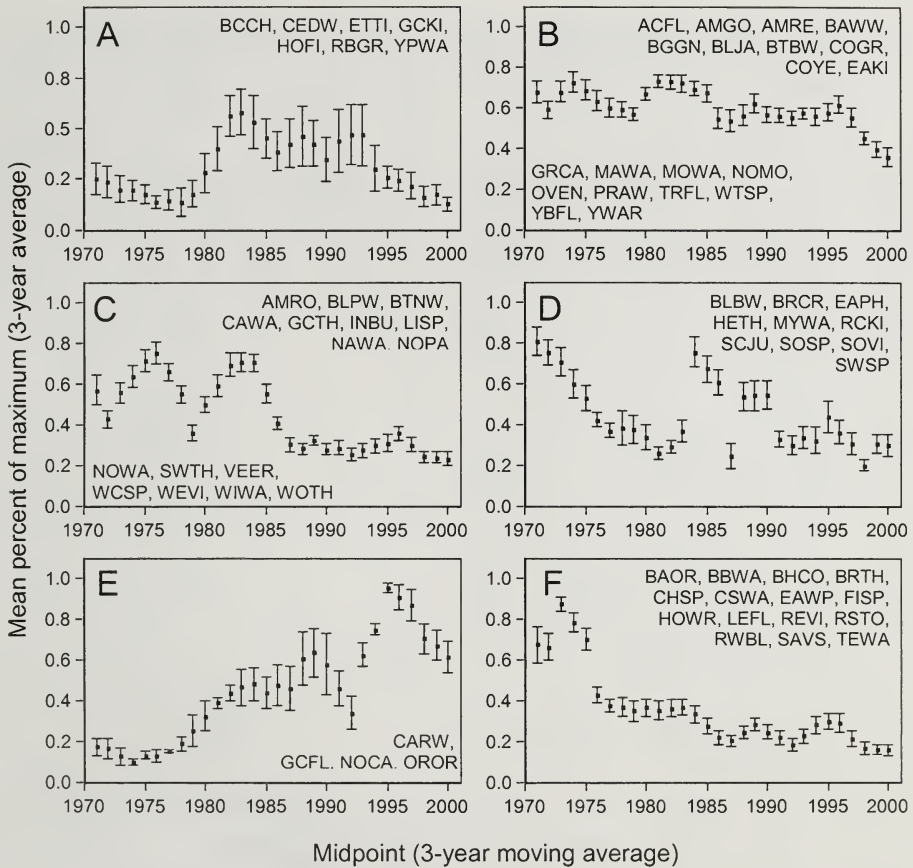


FIG. 5. Major patterns of change in spring capture rates of 72 species in coastal Massachusetts, 1970–2001. Error bars represent ± 1 SE. Species contributing to each plot are indicated with four-letter banding codes; see Appendix.

gan et al. 1992), were grouped together during both spring (Fig. 5E) and fall (Fig. 6C) migrations.

We speculate that at least some of the clustering results (and, therefore, underlying trend patterns) may reflect local weather conditions that would have influenced capture rates of species with similar migration periods. There were significant differences among mean migration dates for each of the six clusters (Fig. 7; Wilcoxon rank sum test; spring: $\chi^2 = 19.34$, $df = 5$, $P = 0.002$; fall: $\chi^2 = 16.12$, $df = 5$, $P = 0.007$). During spring, most species assigned to clusters A and D (Fig. 5A, D) were relatively early migrants, with mean migration dates of 7 May (SE = 4.5 days) and 3 May (SE = 3.4 days), respectively; both of these groups showed somewhat elevated capture rates during the mid to late 1980s, possibly

suggesting that during several years in this time period weather conditions caused larger-than-normal numbers of these species to be present in coastal Massachusetts. Similarly, most species assigned to fall cluster A (Fig. 6A) were relatively late migrants, with a mean migration date of 9 October (SE = 3.3 days); the relatively high capture rates that characterized this group during the early 1970s may have reflected local weather conditions that affected any species with a peak migration period in early October.

Nonetheless, we hesitate to try and provide further explanations for the species "memberships" in each of these groupings. Instead, we prefer to emphasize a more general perspective, noting that only one of the six trend plots from each migration period (spring: Fig. 5E; fall: Fig. 6C) showed obvious increases in

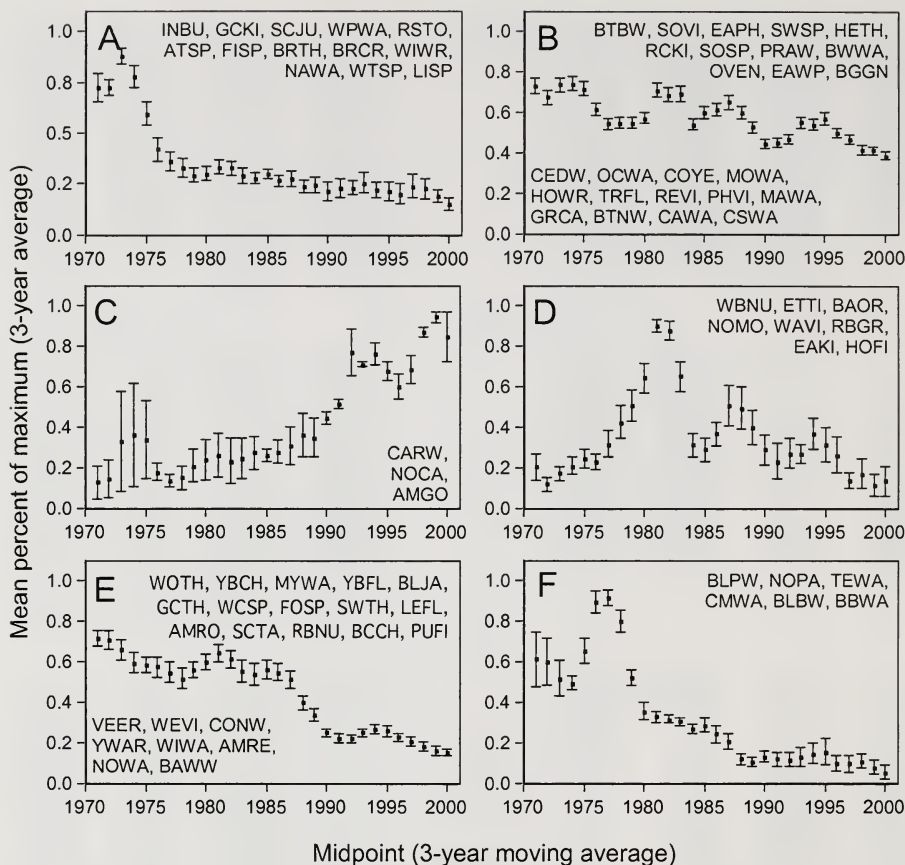


FIG. 6. Major patterns of change in fall capture rates of 78 species in coastal Massachusetts, 1970–2001. Error bars represent ± 1 SE. Species contributing to each plot are indicated with four-letter banding codes; see Appendix.

capture rates. Four of the plots from each migration period (spring: Fig. 5B–D, F; fall: Fig. 6A–B, E–F) showed decreasing trends in capture rates. One plot from each migration period was characterized by peak capture rates during the early to mid 1980s, with comparably low rates before and after this time period (spring: Fig. 5A; fall: Fig. 6D).

DISCUSSION

The Breeding Bird Survey is widely recognized as a primary source of information regarding conservation priorities for North American birds (Geissler and Noon 1981, Butcher et al. 1993, Smith et al. 1993, James et al. 1996, Carter et al. 2000), yet relatively few studies have attempted to validate its conclusions via independent, alternative monitoring schemes. Hussell et al. (1992) compared

a migration index from 1961 to 1988 at Long Point, Ontario with BBS trends in that province and obtained positive correlations, as did Francis and Hussell (1998) in Ontario. Other multiple-year comparisons with BBS data have included intensive counts in Quebec (Jobin et al. 1996) and migration monitoring at Southeast Farallon Island, California (Pyle et al. 1994) and at Point Reyes, California (Ballard et al. 2003). In this paper we present results from a long-term study based on standardized mist-net capture efforts during fall and spring migrations in coastal Massachusetts, and compare these data with estimates of population trends obtained by Sauer et al. (2001) in their analysis of BBS data.

At first glance it would appear that there is good agreement between our results and BBS analyses. There were strong correlations be-

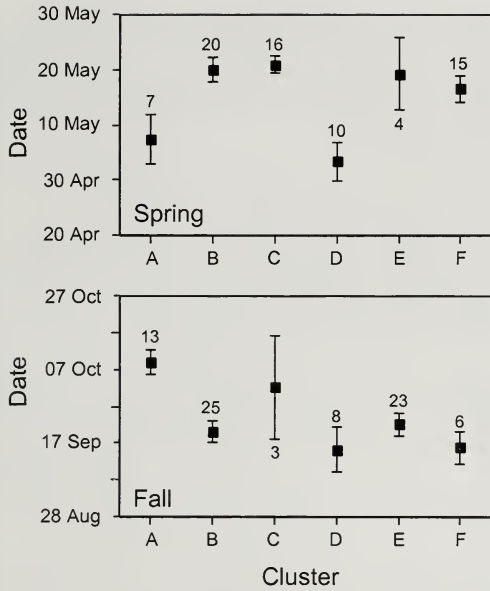


FIG. 7. Mean migration dates during spring and fall for clusters derived from capture trends. Cluster letters correspond with those shown in Fig. 5 (spring) and Fig. 6 (fall). Error bars represent ± 1 SE.

tween population trends observed in each of the three BBS strata considered here and changes in Manomet capture rates between 1970–1985 and 1986–2001, suggesting that both methods do, in fact, reflect changes in regional breeding populations. For example, Least Flycatcher was the only species to decline significantly in all three northeastern BBS strata, and it showed a significant decline in capture rate during fall at Manomet. Of 10 species for which significant declines were noted in two of three northeastern BBS strata, we found significant declines in capture rates during at least one of the two migration seasons for 7 (Eastern Kingbird, Wood Thrush, Common Yellowthroat, Eastern Towhee, Field Sparrow, White-throated Sparrow, and Purple Finch); 2 of the other species (Eastern Wood-Pewee and Common Grackle) declined non-significantly at Manomet, while Great Crested Flycatcher showed a non-significant increase based on migration data. Of 23 species for which the BBS showed significant population declines in at least one of the three physiographic strata considered here, 18 (78%) also showed significant declines in capture rates during spring and/or fall migration.

Yet the situation is more complex than these comparisons might suggest. In many cases our study failed to detect increasing population trends indicated by the BBS. Of 16 species shown by Sauer et al. (2001) to have had significant increases in at least one of the physiographic strata considered here, we found significantly increased capture rates in only 1 (Northern Cardinal). Furthermore, we observed significant declines in capture rates during spring and/or fall migration for five species found by the BBS to be exhibiting significant population increases in at least one of the three physiographic strata [Yellow-bellied Flycatcher, Red-eyed Vireo, Gray Catbird, Yellow-rumped (Myrtle) Warbler, and Ovenbird].

In our study we found significantly declining capture rates during one or both migration periods in 54 of 87 species (62%), but only 5 species (6%) showed significant increases. Among the 37 of these species for which reliable BBS results were available from at least one of the northeast's physiographic strata, Sauer et al. (2001) found significant declines in 22 cases (59%) and significant increases in 15 (41%); Great Crested Flycatcher and Gray Catbird showed opposite significant trends in different physiographic strata. These contrasts suggest that factors in addition to changes in breeding populations may be confounding the relationship with capture rates observed during migration.

We especially note that the patterns we describe here could have emerged if captures of most species we sampled during migration were somehow being reduced, over time, by factors unrelated to actual changes in breeding populations. For example, long-term changes in climate conceivably could cause shifts in regional weather patterns that, in turn, might systematically affect the number of migrants appearing in coastal Massachusetts (Moore et al. 1993). However, we are not aware of any evidence of long-term increases in migration captures at established banding operations east of the Mississippi that might be expected if actual migration patterns were changing. Or, as the vegetation at Manomet has matured since 1970, some species of migrants may now move through the study area at heights where they simply avoid making contact with the nets (2.6 m in height) (Remsen and Good 1996); species that would continue to be ac-

tive primarily within 3 m of the ground, even in the presence of higher canopy cover, might be avoiding the site because of its generally more forested aspect (Moore et al. 1993).

Conversely, the BBS results may themselves be subject to error due to the effects of roadside bias (Temple and Wiens 1989, Keller and Fuller 1995) or short count period (Welsh 1995, Jobin et al. 1996); thus, the trend estimates by Sauer et al. (2001) may not necessarily provide a "gold standard" by which to validate Manomet's migration count results. It is also quite possible that a species could be increasing in one BBS stratum and decreasing in another, or showing conflicting trends within different regions of a single stratum—any of which could confuse the relationship between trends shown by the BBS and migration monitoring data sets. One of the three BBS strata considered here, the eastern Spruce-Hardwood forest, is so large (353,538 km²; Rosenberg and Hodgman 2000) that presentation of a single trend to represent this entire area seems fraught with uncertainty at least equal to our lack of knowledge about the detailed breeding locations of migrants passing through Manomet.

At this point we have no way of further assessing these possible explanations. Certainly capture rates of migrants at Manomet during spring and fall have, in many cases, changed substantially from 1970 to 2001, and the vast majority of these changes have been declines. Migration count data from other studies also indicate long-term declines in New England birds; for example, Hill and Hagan (1991) found that spring surveys of 26 Neotropical migrants in Middlesex and Essex counties of Massachusetts declined, on average, nearly 1% per year from 1954 to 1987. Personal comments from several banders familiar with the location for 30+ years all indicate that there are fewer birds in recent years at Manomet and in New England generally.

Many of the declines documented at Manomet coincide with declines in breeding populations reported by the most reliable BBS data. Nonetheless, there are some apparent inconsistencies between results of the two analyses that we cannot explain. It appears likely that a combination of factors have influenced the number of migrants captured at Manomet since 1970. We believe, however, that the pre-

ponderance of data suggests long-term population declines in a wide variety of both Neotropical and shorter-distance migrants that greatly exceed the few increases that have been observed.

ACKNOWLEDGMENTS

It is impossible for us to name all of the contributors to this project, many of whom have given their time faithfully since the late 1960s. Hosts of students and volunteers have foregone sleep and decent salaries in order to spend their days walking net lanes. The trustees and friends of Manomet Center for Conservation Sciences made this work possible through unflinching personal and financial assistance. We deeply appreciate the support that all of you have given; from Cranberry Hill to Stage Point, your enthusiasm and dedication will always endure. Thank you, C. J. Ralph, C. S. Robbins, and an anonymous reviewer provided helpful comments on a preliminary draft of the manuscript. We dedicate this paper to K. Anderson and those initial banders whose vision and passion gave birth to Manomet Bird Observatory.

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APPENDIX. Banding codes, scientific names, and migration periods of species referred to in text. For each season, the limits of sampling window (1st and 99th percentiles) are given in parentheses following the mean date of migration (all years combined). Dashes (—) indicate species-season combinations (such as fall Acadian Flycatcher) that failed to meet analysis criteria described in Methods.

Code	Common name	Scientific name	Spring	Fall
EAWP	Eastern Wood-Pewee	<i>Contopus virens</i>	31 May (13 May–14 Jun)	10 Sep (16 Aug–10 Oct)
YBFL	Yellow-bellied Flycatcher	<i>Empidonax flaviventris</i>	02 Jun (22 May–15 Jun)	06 Sep (17 Aug–27 Sep)
ACFL	Acadian Flycatcher	<i>Empidonax virescens</i>	31 May (13 May–15 Jun)	—
TRFL	Willow/Alder Flycatcher	<i>Empidonax traillii</i> & <i>E. alnorum</i>	02 Jun (19 May–15 Jun)	02 Sep (16 Aug–30 Sep)
LEFL	Least Flycatcher	<i>Empidonax minimus</i>	21 May (05 May–11 Jun)	04 Sep (17 Aug–05 Oct)
EAPH	Eastern Phoebe	<i>Sayornis phoebe</i>	25 Apr (15 Apr–05 Jun)	21 Sep (16 Aug–25 Oct)
GCFL	Great Crested Flycatcher	<i>Myiarchus crinitus</i>	06 Jun (12 May–15 Jun)	—
EAKI	Eastern Kingbird	<i>Tyrannus tyrannus</i>	25 May (10 May–15 Jun)	25 Aug (15 Aug–20 Sep)
WEVI	White-eyed Vireo	<i>Vireo griseus</i>	21 May (29 Apr–15 Jun)	15 Sep (15 Aug–25 Oct)
SOVI	Blue-headed Vireo	<i>Vireo solitarius</i>	10 May (26 Apr–31 May)	05 Oct (10 Sep–29 Oct)
WAVI	Warbling Vireo	<i>Vireo gilvus</i>	—	11 Sep (17 Aug–07 Oct)
PHVI	Philadelphia Vireo	<i>Vireo philadelphicus</i>	—	16 Sep (23 Aug–21 Oct)
REVI	Red-eyed Vireo	<i>Vireo olivaceus</i>	30 May (14 May–13 Jun)	20 Sep (22 Aug–25 Oct)
BLJA	Blue Jay	<i>Cyanocitta cristata</i>	15 May (20 Apr–11 Jun)	30 Sep (16 Aug–09 Nov)
BCCH	Black-capped Chickadee	<i>Poecile atricapillus</i>	08 May (16 Apr–08 Jun)	14 Oct (23 Aug–11 Nov)
ETTI	Tufted Titmouse	<i>Baeolophus bicolor</i>	28 Apr (15 Apr–09 Jun)	12 Oct (31 Aug–10 Nov)
RBNU	Red-breasted Nuthatch	<i>Sitta canadensis</i>	—	23 Sep (18 Aug–02 Nov)
WBNU	White-breasted Nuthatch	<i>Sitta carolinensis</i>	—	07 Oct (17 Aug–14 Nov)
BRCR	Brown Creeper	<i>Certhia americana</i>	25 Apr (15 Apr–07 Jun)	09 Oct (11 Sep–04 Nov)
CARW	Carolina Wren	<i>Thryothorus ludovicianus</i>	16 May (15 Apr–14 Jun)	06 Sep (15 Aug–05 Nov)
HOWR	House Wren	<i>Troglodytes aedon</i>	15 May (26 Apr–13 Jun)	12 Sep (17 Aug–22 Oct)
WIWR	Winter Wren	<i>Troglodytes troglodytes</i>	—	11 Oct (18 Sep–10 Nov)
GCKI	Golden-crowned Kinglet	<i>Regulus satrapa</i>	22 Apr (15 Apr–06 May)	15 Oct (23 Sep–12 Nov)
RCKI	Ruby-crowned Kinglet	<i>Regulus calendula</i>	29 Apr (17 Apr–17 May)	13 Oct (18 Sep–11 Nov)
BGGN	Blue-gray Gnatcatcher	<i>Poliophtila caerulea</i>	01 May (17 Apr–19 May)	09 Sep (16 Aug–03 Nov)
VEER	Veery	<i>Catharus fuscescens</i>	20 May (05 May–08 Jun)	11 Sep (20 Aug–10 Oct)
GCTH	Gray-cheeked/Bicknell's Thrush	<i>Catharus minimus</i> & <i>C. bicknelli</i>	27 May (14 May–12 Jun)	01 Oct (13 Sep–03 Nov)
SWTH	Swainson's Thrush	<i>Catharus ustulatus</i>	26 May (12 May–10 Jun)	24 Sep (30 Aug–22 Oct)
HETH	Hermits Thrush	<i>Catharus guttatus</i>	29 Apr (16 Apr–19 May)	20 Oct (26 Sep–14 Nov)
WOTH	Wood Thrush	<i>Hylocichla mustelina</i>	16 May (04 May–06 Jun)	18 Sep (18 Aug–26 Oct)
AMRO	American Robin	<i>Turdus migratorius</i>	02 May (15 Apr–13 Jun)	26 Sep (16 Aug–12 Nov)
GRCA	Gray Catbird	<i>Dumetella carolinensis</i>	19 May (03 May–12 Jun)	09 Sep (15 Aug–18 Oct)
NOMO	Northern Mockingbird	<i>Mimus polyglottos</i>	08 May (17 Apr–07 Jun)	13 Sep (16 Aug–12 Nov)
BRTH	Brown Thrasher	<i>Toxostoma rufum</i>	10 May (20 Apr–05 Jun)	25 Sep (15 Aug–31 Oct)
CEDW	Cedar Waxwing	<i>Bombycilla cedrorum</i>	26 May (21 Apr–15 Jun)	02 Oct (17 Aug–10 Nov)
BWWA	Blue-winged Warbler	<i>Vermivora pinus</i>	—	03 Sep (16 Aug–24 Oct)
TEWA	Tennessee Warbler	<i>Vermivora peregrina</i>	23 May (13 May–03 Jun)	20 Sep (19 Aug–28 Oct)
OCWA	Orange-crowned Warbler	<i>Vermivora celata</i>	—	15 Oct (25 Sep–14 Nov)

APPENDIX. Continued.

Code	Common name	Scientific name	Spring	Fall
NAWA	Nashville Warbler	<i>Vermivora ruficapilla</i>	16 May (30 Apr–10 Jun)	23 Sep (17 Aug–31 Oct)
NOPA	Northern Parula	<i>Parula americana</i>	19 May (02 May–09 Jun)	29 Sep (25 Aug–30 Oct)
YWAR	Yellow Warbler	<i>Dendroica petechia</i>	21 May (05 May–10 Jun)	29 Aug (15 Aug–02 Oct)
CSWA	Chestnut-sided Warbler	<i>Dendroica pensylvanica</i>	22 May (03 May–12 Jun)	06 Sep (17 Aug–22 Oct)
MAWA	Magnolia Warbler	<i>Dendroica magnolia</i>	24 May (10 May–10 Jun)	18 Sep (25 Aug–22 Oct)
CMWA	Cape May Warbler	<i>Dendroica tigrina</i>	—	05 Sep (16 Aug–13 Oct)
BTBW	Black-throated Blue Warbler	<i>Dendroica caerulescens</i>	18 May (05 May–04 Jun)	25 Sep (23 Aug–25 Oct)
MYWA	Yellow-rumped (Myrtle) Warbler	<i>Dendroica c. coronata</i>	06 May (16 Apr–26 May)	18 Oct (24 Sep–15 Nov)
BTNW	Black-throated Green Warbler	<i>Dendroica virens</i>	22 May (03 May–13 Jun)	22 Sep (21 Aug–31 Oct)
BLBW	Blackburnian Warbler	<i>Dendroica fusca</i>	26 May (13 May–10 Jun)	09 Sep (21 Aug–19 Oct)
PRAW	Prairie Warbler	<i>Dendroica discolor</i>	13 May (26 Apr–04 Jun)	06 Sep (16 Aug–21 Oct)
WPWA	Palm Warbler (western)	<i>Dendroica p. palmarum</i>	—	06 Oct (08 Sep–12 Nov)
YPWA	Palm Warbler (yellow)	<i>Dendroica p. hypochrysea</i>	28 Apr (16 Apr–14 May)	—
BBWA	Bay-breasted Warbler	<i>Dendroica castanea</i>	23 May (13 May–07 Jun)	04 Sep (17 Aug–10 Oct)
BLPW	Blackpoll Warbler	<i>Dendroica striata</i>	28 May (12 May–15 Jun)	26 Sep (03 Sep–29 Oct)
BAWW	Black-and-White Warbler	<i>Mniotilta varia</i>	15 May (30 Apr–05 Jun)	07 Sep (15 Aug–18 Oct)
AMRE	American Redstart	<i>Setophaga ruticilla</i>	28 May (12 May–13 Jun)	09 Sep (16 Aug–13 Oct)
OVEN	Ovenbird	<i>Seiurus aurocapilla</i>	19 May (03 May–05 Jun)	08 Sep (16 Aug–24 Oct)
NOWA	Northern Waterthrush	<i>Seiurus noveboracensis</i>	19 May (03 May–05 Jun)	07 Sep (16 Aug–17 Oct)
CONW	Connecticut Warbler	<i>Oporornis agilis</i>	—	19 Sep (31 Aug–16 Oct)
MOWA	Mourning Warbler	<i>Oporornis philadelphia</i>	03 Jun (21 May–15 Jun)	09 Sep (15 Aug–17 Oct)
COYE	Common Yellowthroat	<i>Geothlypis trichas</i>	22 May (06 May–10 Jun)	11 Sep (16 Aug–27 Oct)
WIWA	Wilson's Warbler	<i>Wilsonia pusilla</i>	23 May (11 May–08 Jun)	11 Sep (21 Aug–20 Oct)
CAWA	Canada Warbler	<i>Wilsonia canadensis</i>	28 May (13 May–11 Jun)	01 Sep (16 Aug–28 Sep)
YBCH	Yellow-breasted Chat	<i>Icteria virens</i>	—	19 Sep (21 Aug–06 Nov)
SCTA	Scarlet Tanager	<i>Piranga olivacea</i>	—	13 Sep (16 Aug–21 Oct)
RSTO	Eastern Towhee	<i>Pipilo erythrophthalmus</i>	08 May (20 Apr–05 Jun)	27 Sep (16 Aug–05 Nov)
ATSP	American Tree Sparrow	<i>Spizella arborea</i>	—	05 Nov (16 Oct–16 Nov)
CHSP	Chipping Sparrow	<i>Spizella passerina</i>	09 May (21 Apr–03 Jun)	—
FISP	Field Sparrow	<i>Spizella pusilla</i>	07 May (19 Apr–12 Jun)	21 Oct (02 Sep–14 Nov)
SAVS	Savannah Sparrow	<i>Passerculus sandwichensis</i>	07 May (16 Apr–31 May)	—
FOSP	Fox Sparrow	<i>Passerella iliaca</i>	—	29 Oct (08 Oct–14 Nov)
SOSP	Song Sparrow	<i>Melospiza melodia</i>	25 Apr (15 Apr–09 Jun)	29 Sep (16 Aug–09 Nov)
LISP	Lincoln's Sparrow	<i>Melospiza lincolnii</i>	22 May (05 May–09 Jun)	01 Oct (03 Sep–29 Oct)
SWSP	Swamp Sparrow	<i>Melospiza georgiana</i>	11 May (17 Apr–04 Jun)	12 Oct (16 Sep–09 Nov)
WTSP	White-throated Sparrow	<i>Zonotrichia albicollis</i>	04 May (18 Apr–22 May)	10 Oct (13 Sep–12 Nov)
WCSP	White-crowned Sparrow	<i>Zonotrichia leucophrys</i>	14 May (30 Apr–26 May)	12 Oct (20 Sep–31 Oct)
SCJU	Dark-eyed (Slate-colored) Junco	<i>Junco h. hyemalis</i>	21 Apr (15 Apr–17 May)	18 Oct (14 Sep–14 Nov)

APPENDIX. Continued.

Code	Common name	Scientific name	Spring	Fall
NOCA	Northern Cardinal	<i>Cardinalis cardinalis</i>	04 May (15 Apr–12 Jun)	03 Oct (16 Aug–12 Nov)
RBGR	Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	18 May (26 Apr–05 Jun)	12 Sep (18 Aug–24 Oct)
INBU	Indigo Bunting	<i>Passerina cyanea</i>	25 May (25 Apr–14 Jun)	30 Sep (19 Aug–31 Oct)
RWBL	Red-winged Blackbird	<i>Agelaius phoeniceus</i>	11 May (18 Apr–12 Jun)	—
COGR	Common Grackle	<i>Quiscalus quiscula</i>	09 May (18 Apr–13 Jun)	—
BHCO	Brown-headed Cowbird	<i>Molothrus ater</i>	03 May (15 Apr–13 Jun)	—
OROR	Orchard Oriole	<i>Icterus spurius</i>	18 May (10 May–03 Jun)	—
BAOR	Baltimore Oriole	<i>Icterus galbula</i>	20 May (09 May–14 Jun)	28 Aug (15 Aug–09 Oct)
PUFI	Purple Finch	<i>Carpodacus purpureus</i>	—	03 Oct (21 Aug–05 Nov)
HOFI	House Finch	<i>Carpodacus mexicanus</i>	08 May (15 Apr–14 Jun)	12 Sep (16 Aug–16 Nov)
AMGO	American Goldfinch	<i>Carduelis tristis</i>	19 May (18 Apr–15 Jun)	25 Oct (20 Aug–15 Nov)

SUNRISE NEST ATTENDANCE AND AGGRESSION BY LEAST BELL'S VIREOS FAIL TO DETER COWBIRD PARASITISM

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ABSTRACT.—We video-recorded three, natural, brood-parasitism events by Brown-headed Cowbirds (*Molothrus ater*) at nests of Least Bell's Vireos (*Vireo bellii pusillus*). All instances occurred near dawn, during both egg-laying and incubation stages of the nesting cycle. In each case, an adult vireo was on the nest when the female cowbird arrived. Both members of each parasitized pair vigorously attacked the intruding cowbird, but in no encounter did a pair of vireos successfully defend its nest from parasitism. Thus, Least Bell's Vireos in our study were unable to prevent a female cowbird from parasitizing their nests once the cowbird had reached the nest. Received 16 October 2003, accepted 1 April 2004.

There are several ways in which potential hosts may protect a nest from the detrimental impacts of brood parasitism. Two strategies may prevent a cowbird from laying: nest sitting (rushing to the nest and sitting in it; Hobson and Sealy 1989, Gill and Sealy 1996) and aggression directed at the intruding cowbird (Robertson and Norman 1977, Briskie et al. 1990). The effectiveness of such behaviors in deterring parasitism is unclear. The findings of Sealy et al. (1998) suggest that these behaviors do not thwart parasitism. However, J. M. Budnik (pers. comm.) video-recorded a Brown-headed Cowbird (*Molothrus ater*) laying an egg on the back of a midwestern Bell's Vireo (*Vireo bellii bellii*) that refused to leave the nest, and several times observed vireo pairs preventing cowbirds from laying by physically attacking and driving them away (Budnik 1999, Budnik et al. 2001).

After a nest has been parasitized, the most effective anti-parasite responses by the host are to (1) eject the egg from the nest (Rothstein 1976, Sealy and Bazin 1995), or (2) bury the egg (Clark and Robertson 1981, Sealy 1995). A third strategy is that of abandoning the nest and re-nesting, but the effectiveness

of this strategy varies (Graham 1988, Hosoi and Rothstein 2000, Kus 2002).

Nest-attendance behavior by potential hosts during times when cowbirds may lay eggs is an important consideration when examining a host's defense capability (Neudorf and Sealy 1994, Clotfelter and Yasukawa 1999). Scott (1991) and Neudorf and Sealy (1994) found that Brown-headed Cowbirds lay near (usually before) sunrise during the laying stage of the nesting cycle. A host that is vigilant near the nest at these times may be able to defend its nest better than a host that is not attending its nest (Neudorf and Sealy 1994, Clotfelter and Yasukawa 1999). However, Sealy et al. (2000) found that sunrise nest attendance was a function of the onset of incubation rather than a nest-defense strategy.

Least Bell's Vireo (*V. b. pusillus*) is a federally endangered songbird that is heavily parasitized throughout most of its current range in California (Franzreb 1989; Kus 1999, 2002). Consequently, extensive cowbird-trapping programs have been instituted within the geographic range of this vireo. As Least Bell's Vireo is a recent host, co-occurring with cowbirds only during the last century (Mayfield 1965), it may lack natural defenses against parasitism. Least Bell's Vireos only rarely bury cowbird eggs (BEK unpubl. data), and, like many other small hosts, including the western subspecies of Warbling Vireo (*V. gilvus swainsonii*; S. G. Sealy pers. comm.), Least Bell's Vireos are probably unable to grasp- or puncture-eject cowbird eggs (Rothstein 1975a, Spaw and Rohwer 1987, Rohwer and Spaw 1988). Least Bell's Vireos abandon parasitized nests, but they do so at a much

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lower rate (mean = 29%, $n = 207$; Kus 1999) than the nominate subspecies, *V. b. bellii* [74%, $n = 43$ (Parker 1999); 51%, $n = 63$, (Budnik et al. 2001)], and nest desertion and re-nesting by Least Bell's Vireos is not currently an effective defense against the impacts of parasitism (Kus 2002). Nothing is known about the ability of Least Bell's Vireos to deter parasitism through nest defense.

We video-recorded natural parasitism events of Least Bell's Vireos by Brown-headed Cowbirds to examine this host's ability to defend its nest and to analyze host responses after being parasitized. The specific questions we addressed were (1) when do Brown-headed Cowbirds lay their eggs in Least Bell's Vireo nests with regard to time of day and stage in the nesting cycle, (2) are Least Bell's Vireos attending the nest when cowbirds arrive to lay an egg, (3) how do Least Bell's Vireos interact with cowbirds at the nest, and (4) do Least Bell's Vireos accept or reject a parasitic egg? We addressed these questions to evaluate whether Least Bell's Vireo may be able to adapt to the pressure of brood parasitism.

METHODS

We monitored 129 Least Bell's Vireo nests along the San Luis Rey River in northern San Diego County, California, during the 2000 breeding season as part of a larger, long-term study of vireo demographics. Cowbirds were not trapped within our study site during this season. We placed cameras at 19 nests of 13 different vireo pairs between 28 April and 7 July. These nests were in early stages of the nesting cycle when Brown-headed Cowbirds typically parasitize nests (Lowther 1993, Sealy 1995). Videotapings were made from 1 day before clutch initiation through the midpoint (day 6) of incubation. We extended videotaping through day 6 of incubation to find if parasitism might occur later in the cycle. Cameras were of two types: Fuhrman Microcams and Christensen Sentinel Systems. Lenses were placed within 1 m of nests, camouflaged by surrounding vegetation. The camera was connected by cable to the recorder, which was hidden 10–20 m away from the nest. The field of view for cameras included the nest and 5–50 cm radii around the nest, depending on where we were able to locate the camera lens. We videotaped nest activity continuously in

time-lapse mode (20 frames/sec) until either the young fledged, or the nest was depredated or abandoned for other reasons, at which time we moved the camera to another nest.

We reviewed video recordings to determine whether an adult vireo was on or near the nest prior to parasitism, whether vireos defended the nest during parasitism attempts, and whether vireos accepted or rejected cowbird eggs after being parasitized. We noted the duration of each encounter between a female cowbird and the pair of vireos (*sensu* the "laying bout" described in Sealy et al. 1995) as well as the actual time each cowbird spent poised in a laying posture on the nest. We reviewed 2-hr segments (from 1 hr before sunrise to 1 hr after sunrise) for each day a camera was located at a nest, up to the midpoint of incubation, targeting the time of day (Scott 1991, Neudorf and Sealy 1994) and stage of the nesting cycle (Lowther 1993, Sealy 1995) when cowbirds typically parasitize nests. We also noted whether an adult vireo roosted on its nest overnight. If an adult was not on the nest within 1 hr before sunrise, we assumed no adult roosted on the nest, and we recorded the time an adult first visited the nest in the morning relative to time of sunrise. We obtained sunrise times from the U.S. Naval Observatory website.

We considered incubation to begin the day after the last egg was laid, although incubation begins with the penultimate egg (BEK pers. obs.). We chose this chronology to allow us to designate days as either laying days or incubation days. For nests parasitized during laying, we left cowbird eggs in place until clutches were complete (6–10 days after parasitism), and then removed them as authorized by federal and state permits. Means are reported \pm SE.

RESULTS

We videotaped three parasitism events by Brown-headed Cowbirds (Table 1). Two events occurred before sunrise, and one took place shortly after sunrise, yielding a mean parasitism-event time of sunrise = 11.0 ± 6.4 min (Table 1). One nest was parasitized on day 4 of incubation, whereas the others were parasitized during laying (Table 1). No nest was abandoned.

In each parasitism event, an adult vireo was

TABLE 1. Characteristics of the nesting stage of videotaped parasitism events at Least Bell's Vireo nests, San Luis Rey River, San Diego County, California, 28 April–7 July 2000.^a

Date of parasitism	Time of parasitism	Duration of encounter	Time cowbird in nest, laying	Nesting stage when parasitized	Clutch size when parasitized	Completed clutch size (vireo eggs only)
6 May	SR ^b – 21 min	42 sec	23 sec	Day 2 of laying	1	4
15 May	SR – 13 min	35 sec	33 sec	Day 3 of laying	2	4
12 June	SR + 1 min	43 sec	23 sec	Day 4 of incubation	2	2

^a Parasitism event at a fourth nest was not recorded on tape due to technical difficulties.

^b SR = sunrise.

still on the nest from the nocturnal roosting/incubation period. Because birds were not marked, we were unable to identify the gender of individuals. Attendant vireos remained on the nest, but were forced off the nest after being pecked repeatedly by the female cowbird. Once ousted from the nest, the vireo attacked the cowbird and was joined by its mate within a few seconds, suggesting the mate was nearby. Although we could not record sound in time-lapse mode, we could see that the vireos were scolding, and we presume that this vocalization is what attracted the second adult vireo. Both vireos scolded, jumped on the cowbird, struck the cowbird while flying by it, tried to pull the cowbird away from the nest, and repeatedly pecked the intruder. One cowbird left the nest on its first attempt, but returned within 6 sec and successfully laid an egg. Encounters between female cowbirds and hosts averaged 40.0 ± 2.5 sec (Table 1). The mean time each cowbird spent on the nest poised in a laying posture was 26.3 ± 3.3 sec (Table 1). No host eggs were removed by cowbirds.

After parasitism, one member of each vireo pair returned to its nest 7–18 sec ($n = 3$ pairs)

after the cowbird left, and resumed normal nest attendance 21–146 sec after parasitism. Upon returning to the nest to brood, the adult inspected the contents prior to sitting in the nest. Pairs parasitized during laying continued laying until completing the typical clutch of four vireo eggs (Brown 1993, Kus 1999). Egg-laying continued at a normal rate of one egg per day, with the exception of one female that did not lay her fourth egg until 5–7 days after her third egg (6–8 days after parasitism). None of the vireo pairs removed the parasitic egg. In the 114 “nest-days” of tapes we reviewed ($n = 19$ nests), there were no encounters with cowbirds other than the three that resulted in parasitism. Thus, we found no instances in which Least Bell's Vireos prevented a cowbird from parasitizing a nest once the cowbird had reached the nest.

Of the 114 nest-days of tapes, there were only 11 instances in which an adult vireo was not on the nest overnight. Of these 11 cases, 4 occurred before laying began, 6 were during laying, and 1 occurred on day 2 of incubation (Table 2). There were no instances in which an adult did not roost on a nest overnight from day 3 of incubation forward. Linear regression

TABLE 2. Frequency of overnight roosting on the nest and arrival times of non-roosting adult Least Bell's Vireos over the nesting cycle, San Luis Rey River, San Diego County, California, 28 April–7 July 2000.

	Day before lay ^a	Day 1 lay	Day 2 lay	Day 3 lay	Day 4 lay	Day 1 inc ^a	Day 2 inc
Adult on nest overnight/total nests observed	0/4	3/5	11/13	9/10	5/6	15/15	13/14
Mean arrival time of non-roosting adult relative to SR ^b \pm SE (min)	+26.0 \pm 13.1	+30.0 \pm 5.0	+16.5 \pm 0.5	+26	+4		-9

^a lay = laying, inc = incubation.

^b SR = sunrise.

of arrival time (relative to sunrise) versus day of nesting cycle demonstrated that adults that did not roost on the nest overnight arrived at the nest earlier in the day as the nesting cycle progressed ($t = -3.859$, $P = 0.018$; Table 2).

DISCUSSION

Our recordings represent the first video documentation of parasitism by Brown-headed Cowbirds of Least Bell's Vireos. Two of the recorded instances of parasitism occurred during the laying stage of the nesting cycle, as is most often reported in the literature (Lowther 1993, Sealy 1995). The third nest was not parasitized until midway through the incubation stage. Although most parasitism occurs during the laying stage, instances of parasitism during the incubation stage are not uncommon (Lowther 1993, Sealy 1995).

As reported elsewhere (Scott 1991, Neudorf and Sealy 1994), Brown-headed Cowbirds laid their eggs around sunrise. This timing of laying is believed to be an adaptation for laying when host adults do not typically attend nests (Scott 1991); however, Neudorf and Sealy (1994) and Sealy et al. (2000) found that some hosts do attend their nests at sunrise. Clotfelter and Yasukawa (1999) suggested that onset of nocturnal incubation early in the nesting cycle may be a strategy by which Red-winged Blackbirds (*Agelaius phoeniceus*) prevent parasitism. Birds roosting or incubating overnight will be on the nest at dawn, when cowbirds lay and, thus, will be able to defend the nest better than if they were away from the nest during a cowbird visit (Neudorf and Sealy 1994, Clotfelter and Yasukawa 1999).

An adult vireo was roosting at the nest or incubating before each parasitism event we videotaped and an adult roosted overnight on nearly every nest-day we observed. All 11 instances in which an adult did not roost on the nest overnight occurred before or during laying, with the exception of one instance that occurred on day 2 of incubation (Table 2). This pattern, the earlier arrival times of non-roosting adults as the nesting cycle progressed (Table 2), and the vireos' inability to defend their nest when present at the time of a cowbird visit, support the conclusion of Sealy et al. (2000): nest attentiveness is more a function of the onset of incubation than an anti-parasite strategy.

Vireos responded aggressively to the female cowbird in each instance of parasitism. However, sitting in the nest and attacking the cowbird did not prevent parasitism, contrary to observations that midwestern Bell's Vireos escaped parasitism with similar behavior (Budnik 1999, Budnik et al. 2001). We are uncertain as to why defense tactics that were effective in the midwestern subspecies failed to deter parasitism in Least Bell's Vireos.

Least Bell's Vireos quickly accepted cowbird eggs. Possible reasons for acceptance may be (1) lack of recognition of the cowbird egg (Rothstein 1975b, 1990; Sealy 1996; Takasu 1998), or (2) vireos may recognize cowbird eggs as foreign but are unable to eject them. If the latter is the case, nest abandonment is the only response to parasitism available to Least Bell's Vireos. Although nest abandonment was not observed in our sample of videotaped nests, Least Bell's Vireos are known to abandon parasitized nests (Kus 1999), albeit it at a low rate (Kus 2002).

When Least Bell's Vireos accept cowbird eggs, the end result, without human intervention (i.e., removal of cowbird eggs from nests), is the failure to produce vireo young (Kus 1999, 2002). Least Bell's Vireos have never been observed to fledge vireo and cowbird young from the same nest (BEK unpubl. data). We recognize that our sample size is small (such data are extremely difficult to obtain); however, all of the vireos in our study failed to deter parasitism. Given the apparent inability to avert parasitism even when attending the nest at sunrise, and the ineffectiveness of nest abandonment and re-nesting in response to parasitism (Kus 2002), Least Bell's Vireos may lack behavioral defenses sufficient to prevent parasitism or its negative impacts once a female cowbird has reached a vireo nest.

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EFFECTS OF FOOD SUPPLEMENTATION ON FEMALE NEST ATTENTIVENESS AND INCUBATION MATE FEEDING IN TWO SYMPATRIC WREN SPECIES

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ABSTRACT.—We examined effects of incubation mate feeding on female incubation behavior and correlates of fitness by providing female Bewick's Wrens (*Thryomanes bewickii*) and House Wrens (*Troglodytes aedon*) with food supplements. Males of these species vary in their rates of feeding; Bewick's Wrens feed their incubating mates frequently, whereas House Wrens seldom engage in this behavior. Average length of incubation bout and nest attentiveness (proportion of time spent on the nest) were higher for supplemented female Bewick's Wrens and House Wrens compared to controls. Furthermore, mates of supplemented Bewick's Wrens provisioned females at lower rates than controls, and their rate of feeding was inversely correlated with ambient temperature. Incubation length and hatching success were not significantly different between treatments for either species. These results suggest that incubation mate feeding can increase female nest attentiveness and perhaps enhance fitness of both males and females. In House Wrens, potential tradeoffs between the benefits of parental care and opportunities to obtain additional mates may explain why males rarely feed incubating females. Received 1 July 2003, accepted 15 March 2004.

In species that exhibit parental care, there is often a division of labor between sexes, with one sex primarily attending the nest. Consequently, trade-offs between offspring development and survival versus parental condition can exist if nest attentiveness is constrained by parental food limitation (Royama 1966). Food brought to the attending adult by the nonattending mate may ameliorate food limitation, and thus, offset these trade-offs (Smith et al. 1989). Feeding of incubating females by mates occurs in more than 40% of North American passerines (Kendeigh 1952) and is most pronounced in cavity nesters. Nonetheless, considerable variation in the rate of incubation mate feeding exists (Martin and Ghalambor 1999).

Traditionally, incubation feeding was thought to maintain the pair bond between mates (Lack 1940, Kluver 1950, Andrew 1961) or represent a premature attempt by males to feed nestlings (Skutch 1953, Nolan

1958, Ricklefs 1974, Johnson and Kermott 1992). Both of these hypotheses have been challenged, and it has been suggested that food delivered to females constitutes an essential nutritional contribution (i.e., the food limitation hypothesis; von Haartman 1958, Royama 1966, Krebs 1970, Smith 1980, Nilsson and Smith 1988).

Experimental tests of the potential adaptive benefit of incubation feeding (in terms of female attentiveness and hatching success) are relatively rare (e.g., Nilsson and Smith 1988, Moreno 1989, Smith et al. 1989). In this study, we examined effects of food supplements on female incubation behavior and correlates of fitness in two sympatric, secondary cavity-nesting species. Bewick's Wren (*Thryomanes bewickii*) and House Wren (*Troglodytes aedon*). Incubation mate feeding is common in Bewick's Wrens (Miller 1941), whereas male House Wrens rarely feed their mates during incubation (Johnson and Kermott 1992). We increased food available to incubating females by providing food supplements inside nest boxes (Nilsson and Smith 1988, Smith et al. 1989). This allowed females to have sole access to food without leaving nest cavities, simulating incubation feeding. If mate feeding constitutes an important contribution to females, we predicted that food supplements would enhance nest attentiveness. If additional food enhances female attentiveness, hatching success should increase and duration

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of incubation should be reduced at supplemented nests relative to controls. If males do monitor female attentiveness, we also predicted they would adjust their rates of mate feeding accordingly and reduce their rate of incubation feeding to highly attentive females provided with food supplements (Smith et al. 1989).

METHODS

Study area and species.—We conducted this study from early April through late August 1997 at the Konza Prairie Biological Station, 10 km south of Manhattan, Kansas (see Zimmerman 1993 for site description). We monitored 152 nest boxes along gallery forests, attenuated gallery forests, and rock-outcrop shrub communities of Konza (Kennedy and White 1996).

Bewick's Wrens are common summer residents and occasional winter residents of the attenuated gallery forest (Zimmerman 1993). In Kansas, Bewick's Wrens are double-brooded; first nests are initiated in early April and second nests are initiated in late May (Farley 1987). Bewick's Wrens are socially monogamous with only a few suspected cases of polygyny; mean clutch size for this population is 6.1 eggs (Kennedy and White 1997). Only female Bewick's Wrens incubate eggs, but males feed their incubating mates and assist in feeding nestlings (Miller 1941).

House Wrens are common summer residents of Konza, using both gallery and attenuated gallery forests (Zimmerman 1993). They are double-brooded, initiating first nests in early May and second nests in late June. House Wrens are considered socially monogamous (Johnson 1998), but the percentage of males that attract secondary females can be as high as 14% in some populations (Soukup and Thompson 1997a). Mean clutch size of first broods is 6.2 eggs, slightly larger than second broods (5.9 eggs; E. D. Kennedy pers. comm.). Only females incubate, but males generally assist in feeding nestlings. The rate of incubation feeding in a Wyoming population of House Wrens was found to be extremely low (0.2 feedings/hr; Johnson and Kermott 1992), but there are few data on this behavior for other populations.

General procedures.—We checked all nest boxes once weekly from early April until late

July to determine clutch initiation dates. Active nests were then visited every 1–2 days to determine presence and number of eggs or nestlings. Initiation of incubation was determined by egg temperature (warm versus cold) and female behavior. Near the expected hatch dates, nests were visited daily to determine hatch date and hatching success.

Food supplementation experiment.—All nests discovered during egg laying were randomly allocated to either food supplemented or control treatments. Nests allocated to the food supplementation treatment were supplied with 15 g of live mealworm larvae (*Tenebrio molitor*) every day (06:00–10:00 CST) during incubation. This amount of food was chosen based on the estimate that a 10.6 g wren expends ~61 kJ/day (Dykstra and Karasov 1993). Assuming that the energy content of mealworms is 11.59 kJ/g (calculated from Bell 1990) and a wren's assimilation efficiency of mealworms is 0.65 (Kacelnik 1984), a female would need to consume 8.2 g of mealworms to satisfy daily energy requirements. Therefore, a 15-g supplement represents a substantial energy contribution to incubating females. Food supplements were placed in plastic feeding dishes (35 mm film canisters; diameter 3.33 cm, height 4.75 cm) hung inside nest boxes above the nest rim (cf. Nilsson and Smith 1988). This allowed us to simulate male provisioning at the nest entrance and enabled the female to obtain food without leaving the nest cavity.

In most cases, mealworms delivered to nests were consumed before our next visit. If food remained in the canister, dead larvae were removed and replaced with fresh larvae. Videotaped observations revealed that three female House Wrens occasionally removed mealworms from their nest box (see also Johnson and Kermott 1992). This behavior was never observed at Bewick's Wren nests. It is unclear whether these female House Wrens consumed larvae outside their nest boxes or removed them without consuming them. Thus, we performed two exploratory analyses when comparing the effects of treatment on House Wrens, one using all nests and the second excluding data from nests where females removed mealworms. Because the results were similar, we present combined data.

To identify the importance of food avail-

ability to female nest attentiveness, incubation behavior was monitored for 2–4 hr per nest from 07:00 to 12:00 by battery-operated video cameras. Each nest was recorded twice: once during early incubation (incubation day 1–6) and once during late incubation (incubation day 7–12). We observed nests twice to increase observation time and reduce effects of potential anomalous observations. Sampling early and late also allowed us to test whether nest attentiveness changed during the incubation period. Tripods were placed 5–10 m from a nest box one day before taping to acclimate adults to the disturbance. From recordings we determined average length of incubation bout (time inside the nest box), average length of recess bout (time outside the nest box), female nest attentiveness (proportion of time inside the nest box), and frequency of mate feedings at the nest. Because videotaped observations were used, we could not determine the number of mate feedings that may have occurred away from the nest site, out of camera range. It should be noted, however, that in some populations the frequency of House Wren mate feedings away from the nest is extremely low (Johnson and Kermott 1992). The extent to which Bewick's Wren males may feed females away from the nest is not known. Temperature at time of taping was obtained from hourly data recorded at a weather station located at the Konza headquarters.

Data analysis.—All statistical analyses were performed using the Statistical Analysis System (SAS Institute, Inc. 1999). Comparisons of clutch size and clutch initiation between food-supplemented and control nests for each species were performed using *t*-tests (PROC TTEST). Correlations between temperature at the time of observation and female nest attentiveness (both species) and male feeding rate (Bewick's Wrens only) were calculated using PROC CORR.

Four dependant variables describing incubation behavior were analyzed in the food supplementation experiment: lengths of incubation and recess bouts, nest attentiveness, and mate-feeding rate. Mean incubation- and recess-bout lengths were calculated for each videotape session by dividing incubation- and recess-bout lengths by the number of incubation and recess bouts taken, respectively. Fe-

male nest attentiveness was defined as the proportion of time the female spent in the nest box. Mate-feeding rate (feedings/hr; Bewick's Wrens only) was calculated by dividing the frequency of mate feedings for a videotape session by the total time. We did not calculate mate-feeding rate for House Wren males because we only observed three instances of this behavior during our videotape sessions. All behavioral response variables were analyzed using repeated measures ANOVA, with food supplementation as the independent variable of interest and species as a blocking variable. Repeated measures ANOVA was used to account for correlation between multiple nest observations of a single nest (PROC MIXED). Least-squared (LS) means and associated *P*-values were obtained using the LSMEANS statement and PDIFF option. Temperature at the time of taping was used as a covariate in the analysis of mate-feeding rate because a significant correlation was found both in our and other studies (Nilsson and Smith 1988, Smith et al. 1989, Halupka 1994). Differences between early and late incubation behavior were analyzed by species using paired *t*-tests (PROC UNIVARIATE).

Two dependant variables correlated with fitness—incubation length and hatching success—were analyzed to determine whether food supplementation potentially increased fitness. Incubation length (INCL) was calculated using hatch date (HD), clutch size (CS), and clutch initiation date (CID):

$$\text{INCL} = \text{HD} - [\text{CID} + (\text{CS} - 1)].$$

Analysis of variance was used to examine differences in incubation length with the same independent variables as described above (PROC MIXED). Hatching success was analyzed using a generalized linear mixed model approach, which is equivalent to a mixed model logistic regression (GLIMMIX Macro; Wolfinger and O'Connell 1993). The success or failure of individual eggs from successful nests (one or more eggs hatched) were response variables, and nests were considered a cluster sample because responses of individual eggs within a nest may be correlated. Standard errors of hatching success were calculated using the Delta method from standard errors computed on the logit scale (Littell et al. 1996).

TABLE 1. Least-square means of incubation behavior of Bewick's Wrens (BW) and House Wrens (HW) that were, or were not, supplied with additional food, northeast Kansas, summer 1997.

Species	Variable	Food supplemented			Control		
		<i>n</i> ^a	\bar{x}	SE	<i>n</i> ^a	\bar{x}	SE
BW	Incubation bout ^b		51.56	6.89		35.33	6.16
	Recess bout ^c	12	9.77	1.70	15	12.77	1.52
	Nest attentiveness ^d		0.82	0.04		0.70	0.04
HW	Incubation bout ^b		30.21	5.97		13.15	6.16
	Recess bout ^c	16	4.78	1.47	15	5.43	1.52
	Nest attentiveness ^d		0.81	0.04		0.71	0.04

^a Number of videotape sessions.

^b Average amount of time females spent in the nest box without leaving (min).

^c Average of time females spent out of the nest box before returning (min).

^d Proportion of time females spent in the nest box.

Male House Wrens without food were observed visiting nest boxes of their mates. We calculated total visits by Bewick's Wren and House Wren males (total visits = feeding trips + nonfeeding trips) and compared total visits of the two species at control nests using repeated measures ANOVA (PROC MIXED). An alpha value of 0.05 was selected to determine significant differences for all tests.

RESULTS

We observed 15 Bewick's Wren nests (7 food supplemented, 8 control) for 53.4 hr, and 17 House Wren nests (9 food supplemented, 8 control) for 64 hr. Neither clutch size nor date of clutch initiation (mean difference, 95% CI) differed between supplemented and control Bewick's Wren nests [clutch size: 0.13 eggs (-1.37, 1.63); clutch initiation date: -2.5 days (-23, 18)]. Similar results were observed for supplemented versus control House Wren nests [clutch size: 0.28 eggs (-0.63, 1.19); clutch initiation date: 2 days (-14, 18)]. No differences were detected between early and late incubation behavior for either species ($P \geq 0.25$).

Temperature was not correlated with female nest attentiveness for either species (Bewick's Wren: $r = 0.16$, $P = 0.42$; House Wren: $r = 0.03$, $P = 0.86$), but was negatively correlated with feeding rates of male Bewick's Wrens ($r = -0.66$, $P < 0.001$). Consequently, temperature was used as a covariate in the analysis of feeding rate. No significant correlation was found between Bewick's Wren mate-feeding rate and female nest attentiveness ($r = -0.23$, $P = 0.24$).

Food-supplemented females had signifi-

cantly longer average incubation bouts ($F_{1,28} = 6.97$, $P = 0.013$) compared to females in control nests (Bewick's Wren, $P = 0.090$; House Wren, $P = 0.057$; Table 1). Average length of recess bout was not significantly different ($F_{1,28} = 1.38$, $P = 0.25$) between supplemented and control nests (Bewick's Wren, $P = 0.20$; House Wren, $P = 0.76$; Table 1). Female Bewick's and House wrens were 18 and 14% (respectively) more attentive to their nest when food-supplemented compared to control females ($F_{1,28} = 8.55$, $P = 0.007$; Bewick's Wren, $P = 0.034$; House Wren, $P = 0.068$; Table 1). Male Bewick's Wrens made an average of 1.1 fewer mate feedings/hr to food-supplemented females compared to control females ($F_{1,13} = 5.06$, $P = 0.042$; Fig. 1A). Furthermore, male Bewick's Wrens made 0.162 more mate feedings/hr for every 1° C drop in ambient temperature ($F_{1,11} = 21.92$, $P < 0.001$). Experimental food supplementation did not explain variation in incubation length ($F_{1,22} = 0.52$, $P = 0.48$; Bewick's Wren, $P = 0.28$; House Wren, $P = 0.93$; Table 2) or hatching success ($F_{1,22} = 0.70$, $P = 0.41$; Bewick's Wren, $P = 0.59$; House Wren, $P = 0.52$; Table 2).

Male House Wrens from control nests made an average of 1.88 (SE = 0.48) total visits/hr to their nest box during our videotape sessions. This did not differ from the average rate of total visits for Bewick's Wren [1.56 (SE = 0.50) total visits/hr; $F_{1,14} = 0.17$, $P = 0.68$; Fig. 1B].

DISCUSSION

The results of our study support the food limitation hypothesis: food provided to incu-

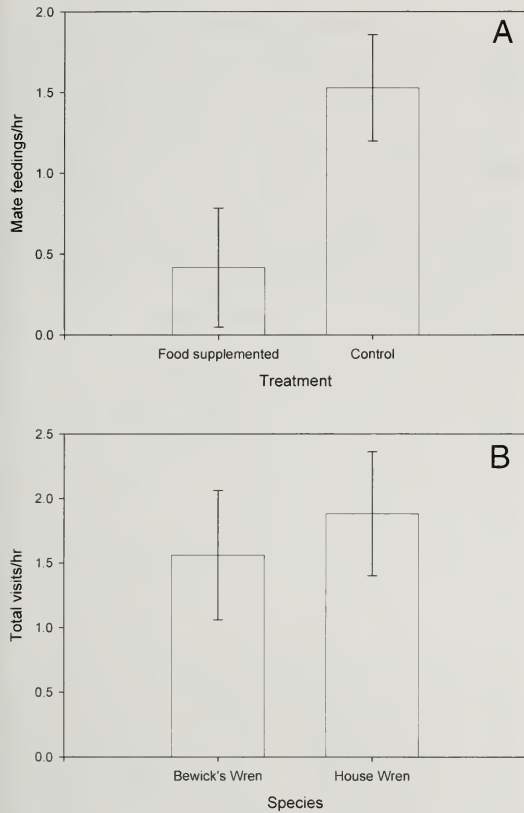


FIG. 1. (A) Feeding rate (feedings/hr \pm 1 SE) of male Bewick's Wrens at food-supplemented and control (no food supplementation) nests during incubation, adjusted using ANCOVA for a mean ambient temperature of 16.78°C. (B) Total visit rate (feedings + non-feedings/hr \pm 1 SE) of male Bewick's Wrens and House Wrens at control nests.

bating females affects their parental effort. Additional food provided to females increased average length of incubation bout and nest attentiveness, suggesting that nest attentiveness is partially determined by the amount of en-

ergy available to the female. Our study supports the results of Smith et al. (1989), who found that nest attentiveness in Pied Flycatchers (*Ficedula hypoleuca*, a species that exhibits mate-feeding behavior) was greater when females were provisioned with additional food.

Bewick's Wren males adjusted rates of incubation feeding to supplemented females: females provided with additional food were fed less often than females not receiving food supplements. Smith et al. (1989) also reported lower male feeding rates to food-provisioned female Pied Flycatchers. Additionally, higher rates of mate feeding in Bewick's Wren males were observed as ambient temperature decreased. This response also has been observed in other species exhibiting incubation feeding (Nilsson and Smith 1988, Smith et al. 1989, Halupka 1994). Our results suggest that provisioning incubating females is costly to male Bewick's Wrens and that they regulate their rate of feeding depending on female nest attentiveness and nutritional state.

Providing adult females of either species with additional food did not result in significant reductions in length of incubation period or in increased hatching success relative to controls, although in Bewick's Wrens there was a trend toward a shorter incubation period for supplemented females (Table 2). Other researchers have documented that mate feeding during incubation can influence these variables (Lyon and Montgomerie 1985, Nilsson and Smith 1988). Averaging 2 years of data (17 nests), Nilsson and Smith (1988) reported significantly earlier hatching (18.9 hr) in food-provisioned Blue Tit (*Parus caeruleus*) nests than in controls. We were unable to measure time of hatching with such precision, but after

TABLE 2. Least-square means of incubation length and hatching success of Bewick's Wrens (BW) and House Wrens (HW) that were supplied with additional food, or not, in northeast Kansas in summer 1997.

Species	Variable	Food supplemented			Control		
		n ^a	\bar{x}	SE	n ^a	\bar{x}	SE
BW	Incubation length ^b	6	12.83	0.77	7	14.00	0.71
	Hatching success ^c		0.78	0.15		0.74	0.13
HW	Incubation length ^b	7	11.67	0.77	6	11.57	0.71
	Hatching success ^c		0.96	0.16		0.82	0.10

^a Sample size of nests used in each analysis.

^b Days of incubation needed to hatch a clutch.

^c Proportion of successfully hatched eggs.

converting our data to hours, we found that hatching was 28 hr earlier in supplemented Bewick's Wren nests than in control nests. Although hatching success was not significantly different between treatment and control nests, it was greater for both species when given additional food: 0.20 and 0.95 additional eggs hatched in food-provisioned Bewick's and House wren nests, respectively. In Blue Tits, Nilsson and Smith (1988) found a significant increase (6.5%) in hatching success among food-provisioned nests. Even though we did not detect a statistical difference in hatching success, at a population level this observed difference might be of ecological importance. Furthermore, if our study had been conducted in years with poor food availability or cooler temperatures, fitness benefits of additional food might have been more apparent (the long term mean temperature for Manhattan, Kansas for May through July 1897–1994, was 18.3°, 23.7°, and 26.6° C; mean temperatures for May through July 1997 were 16.8°, 24.0°, and 27.3° C).

Enhancing nest attentiveness through incubation mate feeding could have other benefits (other than reduced incubation length or increased hatching success), such as serving to reduce intra- and interspecific nest destruction. Nest guarding has been shown to reduce nest predation in other species (Simons 1988, Cavitt 1998), and time available for guarding can be limited by food availability (Cavitt 1998). Thus, if nest destruction by House Wrens is an important source of nest loss for Bewick's Wrens, increased nest attentiveness may further enhance fitness by reducing the probability of nest destruction by House Wrens. Kennedy and White (1996) reported that the percent of failed Bewick's Wren nests caused by House Wrens on our site in other years ranged from 33 to 100%. During our study, however, House Wrens destroyed only one Bewick's Wren nest; thus, we could not test this hypothesis with our data. The nest-destruction hypothesis does not explain the lack of incubation feeding observed in House Wrens, because they are also vulnerable to nest destruction by conspecifics (Johnson 1998). Yet, House Wrens may use other strategies, such as the coordination of nest-guarding activities (Ziolkowski et al. 1997), to reduce nest destruction by conspecifics.

If providing additional food to female House Wrens can enhance nest attentiveness and, potentially, male fitness, why don't males feed their incubating mates more frequently? Several hypotheses have been proposed to explain the lack of incubation mate feeding (Moreno 1989, Johnson and Kermott 1992). The predation hypothesis (Lyon and Montgomerie 1987) proposes that species with a greater risk of nest predation should have lower rates of incubation feeding than species with lower predation risks, because increased trips to the nest may attract attention of predators and increase predation risk (Skutch 1949; Martin 1992, 1996). In fact, incubation feeding rates in a suite of coexisting species was inversely correlated with predation rate (Martin and Ghalambor 1999). Predation is not a likely explanation in the Konza population because we commonly observed male House Wrens visiting their nests during the incubation period without delivering food. Total number of visits made by House Wren males was not significantly different from the total number of trips made by male Bewick's Wrens (Fig. 1B). Thus, the occurrence of non-feeding visits by male House Wrens is not consistent with the nest predation hypothesis.

An alternative explanation for the difference between male House Wrens and Bewick's Wrens is that although food provided to the female is beneficial, other activities may provide greater gains in male fitness (Lifjeld and Slagsvold 1986, Lifjeld et al. 1987). Male House Wrens might, for example, increase fitness by seeking extra-pair copulations and attracting additional mates. Johnson and Kermott (1992) discounted this hypothesis because mate-feeding rates did not differ significantly between males that attempted to attract additional mates and those that did not. However, because House Wren incubation feeding rates are extremely low and variable, detecting any significant difference between males that vary in this behavior would be difficult. Male House Wrens frequently invest time and energy intruding onto adjacent territories (2.02 ± 0.41 intrusions/hr) to obtain extra-pair copulations (Johnson and Kermott 1989). In an Illinois population of House Wrens, Soukup and Thompson (1997b) found a high rate of extra-pair paternity (~27% of all nests sampled) and documented that approximately

14% of males were polygynous. Thus, other activities may enhance fitness of male House Wrens more than improving female attentiveness via mate feeding.

Our results demonstrate that food provided by males to incubating females can be an important factor influencing nest attentiveness and may enhance fitness. The disparity in male mate-feeding rates between these species most likely reflects differences in benefits to male fitness. The ability to maintain high levels of nest attentiveness may have a great effect on the fitness of male Bewick's Wrens because House Wrens are important nest predators. In contrast, benefits of increased nest attentiveness to the fitness of male House Wrens may be outweighed by the benefits of participation in other activities, such as extra-pair copulations and polygamous mating.

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RED-COCKADED WOODPECKER NESTLING PROVISIONING AND REPRODUCTION IN TWO DIFFERENT PINE HABITATS

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ABSTRACT.—We obtained nestling provisioning and reproductive data from 24 Red-cockaded Woodpecker (*Picoides borealis*) groups occupying two different pine habitats—longleaf pine (*Pinus palustris*) and a mixture of loblolly (*P. taeda*) and shortleaf pine (*P. echinata*)—in eastern Texas during 1990 and 1991. Habitat data were collected within 800 m of each group's cavity-tree cluster. Feeding trips per nest and prey biomass per feeding trip were significantly greater in loblolly-shortleaf pine habitat. There were few significant correlations between reproductive/provisioning and habitat variables in either pine habitat. Pines dying from infestation by southern pine beetles (*Dendroctonus frontalis*) were more common in loblolly-shortleaf than in longleaf pine habitat. In addition, adult male Red-cockaded Woodpeckers weighed more in loblolly-shortleaf pine habitat. Indices of southern pine beetle abundance in loblolly-shortleaf pine habitat were negatively correlated with number of feeding trips per nestling, but positively correlated with prey biomass delivered to nestlings. We hypothesize that the greater abundance of southern pine beetles and associated arthropods in loblolly-shortleaf pine habitat, and the resulting higher frequency of dying pines containing an abundant food source, were associated with an elevated prey biomass available to both nestling and adult Red-cockaded Woodpeckers. Received 29 June 2003, accepted 20 April 2004.

The Red-cockaded Woodpecker (*Picoides borealis*) is a cooperatively breeding species that lives in family groups of two or more individuals (Ligon 1970, Walters et al. 1988). Groups include a breeding pair, young of the year, and often one to three other adults, which serve as "helpers." Helpers are usually male offspring from previous nestings and assist the breeding pair with caring for nestlings (Ligon 1970, Lennartz and Harlow 1979). Red-cockaded Woodpeckers are endangered (U.S. Department of Interior 1970) and inhabit open, mature pine (*Pinus* spp.) habitats of the southeastern United States. Populations have become fragmented and isolated due to severe habitat alterations (Costa and Escano 1989, Rudolph and Conner 1994). Cutting of old-growth pine forests and elimination of recurring fire across most of the woodpecker's range are major causes of the species' decline (Jackson 1971, Lennartz et al. 1983). Historically, fire maintained suitable foraging and nesting habitat. Several studies have reported positive indirect effects of fire on Red-cock-

aded Woodpecker fitness through increased arthropod abundance (Provencher et al. 1998, 2001), increased grass and/or forb ground cover (James et al. 1997), and reduced hardwood midstory vegetation (Walters et al. 2002).

Red-cockaded Woodpeckers are known to select larger and older pines as foraging substrates (Engstrom and Sanders 1997, Zwicker and Walters 1999, Walters et al. 2002); such pines are believed to support more arthropods (Hanula et al. 2000), particularly during the breeding season (Conner et al. 2004). Young pine forests may offer suboptimal foraging habitat by providing a reduced prey base, especially in areas surrounding cavity tree clusters (stands of cavity trees occupied by Red-cockaded Woodpecker groups) that have been clearcut or contain dense plantations of young (<30 years) pines. Foraging and provisioning of nestlings may be more difficult in young pine forests, which could have a negative effect on the survivorship of adults and nestlings (Ligon 1970, 1971).

Logically, prey availability during the nesting season has an impact on Red-cockaded Woodpecker reproductive success and adult nutrition. There is little information regarding comparisons of arthropod densities and biomass between longleaf pine (*Pinus palustris*) and loblolly-shortleaf pine (*P. taeda*-*P. echin-*

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ata) habitats. During nesting season, differences in prey availability among habitats dominated by different pine species can impact both reproduction and adult nutrition of Red-cockaded Woodpeckers.

The southern pine beetle (*Dendroctonus frontalis*) is responsible for considerable pine mortality, especially during cyclic epidemics (Conner et al. 2001). Infestations can potentially destroy Red-cockaded Woodpecker foraging habitat and cavity trees. However, during non-epidemic beetle years, woodpeckers can benefit by concentrating foraging activity on dying pines that provide an arthropod-rich food source (Hooper and Lennartz 1981, Schaefer 1996, Bowman et al. 1997). Such ephemeral food sources, while unpredictable, can provide nutritional benefits to both nestlings and adults.

Our objectives were to (1) compare reproductive and provisioning effort in longleaf pine and loblolly-shortleaf pine habitats, (2) determine whether habitat variation affected reproduction and nestling provisioning, and (3) use body mass of adults to assess nutritional status of birds in longleaf pine and loblolly-shortleaf pine habitats.

METHODS

Study areas.—We collected reproductive, nestling provisioning, and vegetation data during the 1990 and 1991 nesting seasons. Study sites were on the Davy Crockett National Forest (DCNF) and the Angelina National Forest (ANF) in eastern Texas (see Conner and Rudolph 1989 for area descriptions). We chose 24 study sites (i.e., 24 woodpecker groups), 8 at DCNF and 16 at ANF. Sites were selected based on the dominant pine species; 11 sites were located in longleaf pine and 13 were located in loblolly-shortleaf pine habitat.

Reproduction and nestling provisioning.—All Red-cockaded Woodpeckers captured at each of the 24 study sites were banded (U.S. Fish and Wildlife Service band and 2–3 color bands) for individual recognition. Birds were visually identified in the field with the aid of binoculars and a 20× spotting scope mounted on a tripod.

Nest monitoring began during the first week of April, about 2 weeks before nesting was expected to commence. If an adult occupied the nest cavity when checked, the tree was

climbed using sectional aluminum ladders; eggs were then counted. If the clutch did not appear complete (normally two to four eggs comprise a complete clutch), it was checked again in a few days. When nestlings were detected, the nest tree was again climbed and young were counted and aged (Ligon 1971).

Provisioning data were collected when nestlings were 8, 20, and 23 days of age. The nest cavity of each woodpecker group was observed for a 3-hr period in the morning, beginning when the breeding male exited the nest. We recorded identity of the adult bringing food, size of each prey item, and time of each feeding. Prey size was visually estimated and categorized as small, medium, or large. An item was considered small if barely visible in the adult's beak. A medium-sized item was estimated at less than one-half of the beak's length. A large item was estimated at more than one-half of the beak's length. We assume that any bias toward larger prey inherent in this procedure was equal among the two pine habitats.

We attempted to obtain a biomass value for each size category. Since it was not possible to collect samples of prey items delivered to nestlings, we collected arthropods similar to those observed being provided in both pine habitats. Samples were obtained from the boles of dead loblolly and shortleaf pines killed by southern pine beetles. These arthropods were separated into small, medium, and large size categories using the same criteria used during provisioning observations. We collected 30 individuals of each size category, determined wet weight (mg), and calculated average weight for each size category. Relative values for prey biomass were calculated using the mean weight of each size category (small = 11.3 mg, medium = 45.6 mg, large = 197.4 mg).

Vegetation and stand area measurements.—Habitat data were collected at each study site within an 800-m radius centered on each woodpecker group's cluster of cavity trees. Forest compartment stand maps were obtained from the ANF and DCNF district offices for those compartments falling within the 800-m radius. Each compartment is comprised of forest stands of varying size. Five dominant or codominant pines were selected within each forest stand within the 800-m radius by

choosing the nearest tree in a random direction from five arbitrary points well-dispersed within the stand. Habitat measurements were taken within an 11.2-m radius (0.04-ha circular plot) centered on each of these five trees (Conner 1980), and means were used to characterize habitat within the forest stand.

Stand age was determined by coring each central tree at breast height (1.3 m) with an increment borer and counting growth rings of the cores. We added 3 years for loblolly pine and shortleaf pine, and 5 years for longleaf pine to account for growth to breast height (Conner and O'Halloran 1987). Stands were categorized as 0–29, 30–49, 50–69, 70–89, or >90 years old. Tree diameter (cm) was measured at breast height (dbh) with calipers and categorized as 0–30, 30.1–40, 40.1–50, or 50.1–70 cm. Surrounding canopy height and midstory height (m) were measured with a range finder. Canopy height was placed into categories of 0–12, 12.1–21, 21.1–27, or 27.1–33 m.

Midstory density was visually estimated and placed into one of five categories: none, sparse, moderate, dense, or very dense. Midstory conditions were considered suitable if height was ≤ 3 m regardless of density, or if density was none to sparse regardless of height. A one-factor metric basal area prism was used to measure basal area (m^2/ha) of pine overstory, hardwood overstory, pine midstory, and hardwood midstory. Pine and hardwood overstory basal areas were placed into categories of 0–9, 9.1–15, 15.1–20, 20.1–25, or 25.1–30 m^2/ha . Pine and hardwood midstory basal areas were categorized as 0–3, 3.1–6, 6.1–9, or 9.1–12 m^2/ha . The area (ha) of each forest stand within 800 m of each nest tree was measured from compartment stand maps with a digitizer, and the percentage of area occupied by each habitat category calculated.

Measurements of southern pine beetle abundance.—Data on southern pine beetle abundance during 1990 and 1991 were obtained from the U.S. Forest Service for each forest compartment where study sites were located. All other causes of mature pine mortality were assumed to be equal between longleaf and loblolly-shortleaf pine habitats. Three variables were used as indices of southern pine beetle abundance in comparing beetle ac-

tivity in longleaf pine versus loblolly-shortleaf pine: (1) the number of active beetle spots (one or more contiguous beetle-infested trees), (2) the number of trees infested (dying pines with fading or red needles, and all or most bark remaining), and (3) the number of hectares affected by infestation. A total for each variable was calculated for the entire forest compartment, even if only a portion of the compartment fell within the 800-m radius circle.

Adult Red-cockaded Woodpecker body mass.—Each adult woodpecker was weighed to the nearest 0.5 g with a 100-g spring scale. Body mass was obtained throughout the year, except during nesting; each bird was weighed once. Birds were captured either in the morning just before exiting the roost cavity, or in the evening just after entering. We realize there is both seasonal and temporal (24-hr) variability in the body mass of a given individual. For each of the two pine habitats, body masses were pooled by sex.

Data analysis.—Data were analyzed using SAS (SAS Institute, Inc. 1988). A significance level of $P = 0.05$ was used in all hypothesis testing. In tests involving habitat variables, stands 0–29 years old, most of which were clearcuts and young pine plantations, were not included in evaluations of available foraging habitat because these stands are considered unsuitable for Red-cockaded Woodpecker foraging (U.S. Fish and Wildlife Service 2003). However, the 0–29 year stand age category is included for comparative purposes.

The 24 Red-cockaded Woodpecker groups observed produced a total of 37 successful (i.e., one or more fledglings) nests during the two nesting seasons. For statistical analyses, a 2-year average of each reproductive variable was used for each group to avoid a repeated measures violation. Comparisons of reproductive variables between pine habitats using repeated measures analyses were not possible because of instances of small sample sizes within years due to some groups not nesting for various reasons, especially in longleaf pine habitat.

Pearson correlation coefficients were used to explore relationships of reproductive and provisioning variables with habitat variables. Two-tailed *t*-tests were used to compare reproductive performance and provisioning ef-

fort between longleaf and loblolly-shortleaf pine. A medium effect size of 0.5 (Cohen 1988) was used in power analyses for statistically non-significant variables.

Two-way ANOVAs (pine type \times habitat variable) on ranked data were used to compare category distribution of each habitat variable (tree age, diameter at breast height, canopy height, suitable/unsuitable midstory, pine overstory basal area, hardwood overstory basal area, pine midstory basal area, and hardwood midstory basal area) between longleaf ($n = 11$) and loblolly-shortleaf ($n = 13$) pine habitats. If the interaction indicated different distributions between the pine habitats, Wilcoxon rank-sum tests were used for each habitat variable category to test for differences between longleaf and loblolly-shortleaf pine.

Two-tailed t -tests were used to compare southern pine beetle abundance and body mass of adult Red-cockaded Woodpeckers between the pine habitats. Pearson correlation coefficients were used to examine relationships between southern pine beetle abundance, and provisioning effort and reproductive performance, within each pine habitat. Adult male body mass, including that of both helpers and breeders, was treated separately from adult female body mass due to differing foraging strategies (Ligon 1968, Hooper and Lennartz 1981).

RESULTS

Nesting effort in relation to pine habitat.—During the two nesting seasons, 24 Red-cockaded Woodpecker groups had a total of 37 successful (i.e., one or more fledglings) nests. For various reasons, not all groups successfully nested. One longleaf clutch was depredated and the group did not reneest. One loblolly-shortleaf group disappeared altogether between years. Eggs at three nests failed to hatch (one in longleaf, two in loblolly-shortleaf). Breeding pairs at five longleaf sites appeared to forgo nesting during 1 of the 2 years. Although unlikely, some clutches may have been initiated and then depredated immediately before we detected them. If so, the birds did not appear to reneest.

Twelve (80%) of 15 successful nests in longleaf pine habitat lacked helpers, and only one helper was present at the remaining 3 (20%) nests. Eleven (50%) of 22 successful

nests in loblolly-shortleaf pine habitat lacked helpers. Of the remaining 11 nests, 10 (45%) had one helper and 1 (5%) had two helpers (one male and one female). For all 24 groups (2 years combined) the average number of helpers per group was 0.4.

During the two nesting seasons, 17 clutches were produced in longleaf pine and 24 in loblolly-shortleaf pine. Clutch size was not recorded in two instances, once in each habitat. The remaining 16 longleaf nests produced a total of 51 eggs ($\bar{x} = 3.19$ eggs/clutch), and 23 loblolly-shortleaf nests produced a total of 78 eggs ($\bar{x} = 3.39$ eggs/clutch). Hatching success based on clutch size was 75% in longleaf pine and 87.3% in loblolly-shortleaf. Hatching success, as measured by the number of nestlings hatched from eggs surviving through the incubation period, was 85.7% (36 nestlings from 42 eggs; $n = 13$ nests) in longleaf habitat and 89.9% (62 nestlings from 69 eggs; $n = 20$ nests) in loblolly-shortleaf habitat. Two clutches in each pine habitat failed to hatch, leaving a total of 15 and 22 broods produced in longleaf and loblolly-shortleaf, respectively. The 15 broods in longleaf produced 24 fledglings ($\bar{x} = 1.60$ fledglings/nest), and the 22 in loblolly-shortleaf produced 42 fledglings ($\bar{x} = 1.91$ fledglings/nest). The initial number of nestlings could not be counted for two broods in each pine habitat. Fledging success subsequent to hatching was 55.6% for the remaining 13 broods in longleaf, and 62.9% for the remaining 20 broods in loblolly-shortleaf habitat.

Considering only woodpecker groups that produced one or more fledglings, all nest productivity measures (with the exception of partial brood loss) and number of adults were slightly higher in loblolly-shortleaf than in longleaf pine habitat; only feeding trips per nest and prey biomass per feeding trip were statistically greater (Table 1). Power analyses revealed that sample sizes in each pine habitat were too small to detect biological significance (medium size effect of 0.5, power = 0.2) for statistically non-significant variables.

A two-way ANOVA was calculated to evaluate the contribution of group size to the number of feeding trips to nests in loblolly-shortleaf and longleaf pine habitats. There was no significant interaction ($F_{2,16} = 0.43$, $P = 0.66$) between group size and pine habitat in relation

TABLE 1. Red-cockaded Woodpecker nesting effort^a (mean \pm SD) in longleaf ($n = 10$)^b and loblolly-shortleaf ($n = 13$) pine habitats in eastern Texas during 1990 and 1991.^c

Nesting variable	Longleaf	Loblolly-shortleaf	<i>t</i>	<i>P</i>
Group size	2.3 \pm 0.4	2.5 \pm 0.5	1.43	0.17
Clutch size	3.3 \pm 0.6	3.5 \pm 0.5	0.91	0.37
Initial brood size ^d	2.9 \pm 0.7	3.0 \pm 0.6	0.53	0.61
Brood size ^e	1.7 \pm 0.5	2.0 \pm 0.4	1.68	0.11
Feedings per nest ^e	31.4 \pm 9.7	43.3 \pm 11.3	2.66	0.015
Feedings per nestling ^e	19.7 \pm 7.1	22.7 \pm 5.4	1.15	0.26
Prey biomass per trip (mg) ^e	73.2 \pm 31.0	116.7 \pm 36.3	3.03	0.006
Number of fledglings	1.7 \pm 0.5	1.9 \pm 0.4	1.41	0.17
Partial brood loss ^{df}	0.3 \pm 0.2	0.2 \pm 0.2	0.59	0.56

^a Only groups that produced at least one fledgling are included in these analyses.

^b Sample size = 10 because one longleaf pine group did not produce at least one fledgling during either year.

^c The total number of nests producing fledglings was 15 at longleaf pine and 22 at loblolly-shortleaf pine sites over the two nesting seasons. The 2 years were averaged for each nesting variable, for each group.

^d Initial brood size and partial brood loss are each unknown in one instance in longleaf pine habitat. Therefore $n = 9$ in longleaf for these two nesting variables.

^e Means based upon observations at 8, 20, and 23 days of nestling age at each nest.

^f Nestling loss between hatching and day 8.

to the number of feeding trips per nest, and group size alone did not influence ($F_{3, 16} = 0.41$, $P = 0.75$) number of feeding trips per nest. These results indicate that differences between the two pine habitats, and not group size, were responsible for the greater number of feeding trips made to nests in loblolly-shortleaf pine habitat.

Mean number of feeding trips per nest was significantly greater in loblolly-shortleaf pine habitat, but mean number of feeding trips per nestling was similar, indicating that individual nestlings were fed at about the same frequency in both pine habitats (Table 1). However, average prey biomass per feeding trip was significantly greater in loblolly-shortleaf than in longleaf pine (Table 1), indicating that nestlings in the former received more food. There were few significant correlations among reproductive/provisioning variables and habitat variables in either pine habitat. Of note was the lack of significant relationships between any of the habitat variables and prey biomass within either pine habitat. Thus, the habitat variables we measured had little or no relationship with size of prey items delivered to nestlings.

Comparison of longleaf and loblolly-shortleaf pine habitats.—The percentage of area occupied by forest stands <30 years old was greater in loblolly-shortleaf than in longleaf pine habitat ($Z = -3.22$, $P = 0.001$; Fig. 1A). This was the result of extensive clear-cutting that occurred during the 1970s and 1980s, as

well as southern pine beetle control cuts in loblolly-shortleaf pine study sites. Cutting seldom occurred in longleaf pine study sites. Forest stands in the 30–49 year ($Z = 2.71$, $P = 0.007$) and 50–69 year ($Z = 2.12$, $P = 0.034$) age categories occupied more area in longleaf pine habitat, whereas stands in the 70–89 year ($Z = -3.62$, $P < 0.001$) age category occupied more area in loblolly-shortleaf pine habitat (Fig. 1A). There was no difference between pine habitats in the percentage of area occupied by the 90–120 year age category ($Z = -1.50$, $P = 0.13$; Fig. 1A). This oldest stand-age category constituted only a small percentage of area within the 800-m radius in both pine habitats.

Loblolly-shortleaf pine contained a higher frequency of stands in the largest dbh category of 50.1–70 cm ($Z = -2.78$, $P = 0.006$) and highest canopy height category of 27.1–33 m ($Z = -3.72$, $P < 0.001$) than did longleaf pine (Figs. 1B and 1C). Conversely, the smaller dbh category of 30.1–40 cm ($Z = 3.63$, $P < 0.001$) and shorter canopy height categories of 12.1–21 m ($Z = 2.11$, $P = 0.035$) and 21.1–27 m ($Z = 2.32$, $P = 0.021$) were more common in longleaf pine (Figs. 1B and 1C).

Comparison of midstory between pine habitats revealed that the percentage of area with suitable midstory conditions was greater in longleaf pine ($Z = 3.74$, $P < 0.001$) and the percentage of area occupied by unsuitable midstory conditions was greater in loblolly-

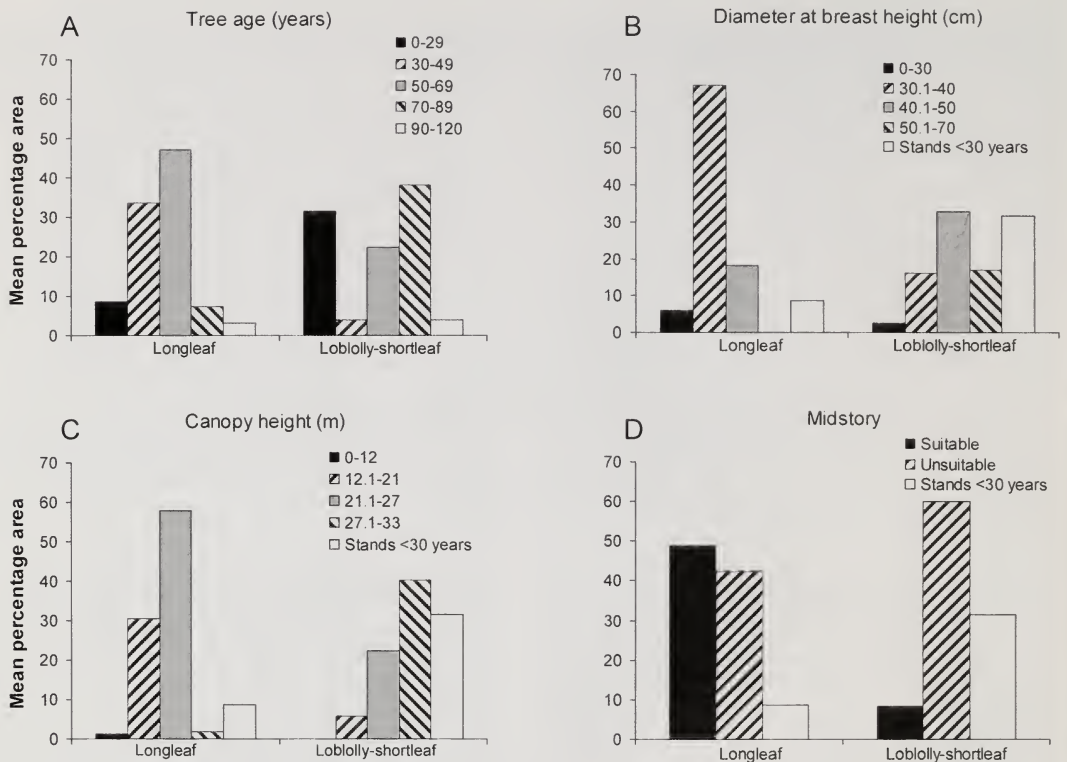


FIG. 1. Mean percentage of area within 800 m of Red-cockaded Woodpecker cavity-tree clusters occupied by each category of (A) tree age, (B) diameter at breast height, (C) canopy height, and (D) midstory in longleaf pine ($n = 11$) and loblolly-shortleaf pine ($n = 13$) sites in eastern Texas, 1990–1991.

shortleaf pine ($Z = -2.17$, $P = 0.030$; Fig. 1D). When habitat of all ages (i.e., including stands <30 years old) within 800 m of woodpecker nest trees was considered, the average percentage of area with unsuitable midstory was 51% for longleaf and 93% for loblolly-shortleaf pine.

Pine overstory basal area was similar between pine habitats with the exception of the 20.1–25 m^2/ha category, which occupied a greater percentage of area in longleaf pine ($Z = 2.62$, $P = 0.009$; Fig. 2A). Trees in the 0–9 m^2/ha hardwood overstory basal area category occupied a greater percentage of area in longleaf than in loblolly-shortleaf pine ($Z = 3.05$, $P = 0.002$). Few forest stands containing overstory hardwoods were within any basal area category greater than 0–9 m^2/ha in either pine habitat (Fig. 2B).

No significant differences were found in any pine midstory basal area category between the two pine habitats ($F_{3, 88} = 1.96$, P

$= 0.13$; Fig. 2C). The percentage of area occupied by the relatively low hardwood midstory basal area category of 0–3 m^2/ha was greater in longleaf pine ($Z = 3.97$, $P < 0.001$). The percentage of area occupied by the greater hardwood midstory basal area categories of 3.1–6 m^2/ha ($Z = -2.89$, $P = 0.004$), 6.1–9 m^2/ha ($Z = -2.13$, $P = 0.033$) and 9.1–12 m^2/ha ($Z = -1.96$, $P = 0.050$; Fig. 2D) were all greater in loblolly-shortleaf pine.

Southern pine beetle influence.—The number of active beetle spots, beetle-infested trees, and total hectares infested with beetles were all significantly greater in loblolly-shortleaf pine habitat (Table 2). At loblolly-shortleaf nests in which at least one fledgling was produced ($n = 22$), number of active beetle spots ($r = 0.48$, $P = 0.022$), beetle trees ($r = 0.45$, $P = 0.036$), and infested hectares ($r = 0.67$, $P < 0.001$) were positively correlated with prey biomass delivered to nestlings. Number of beetle spots ($r = -0.57$, $P = 0.006$), beetle

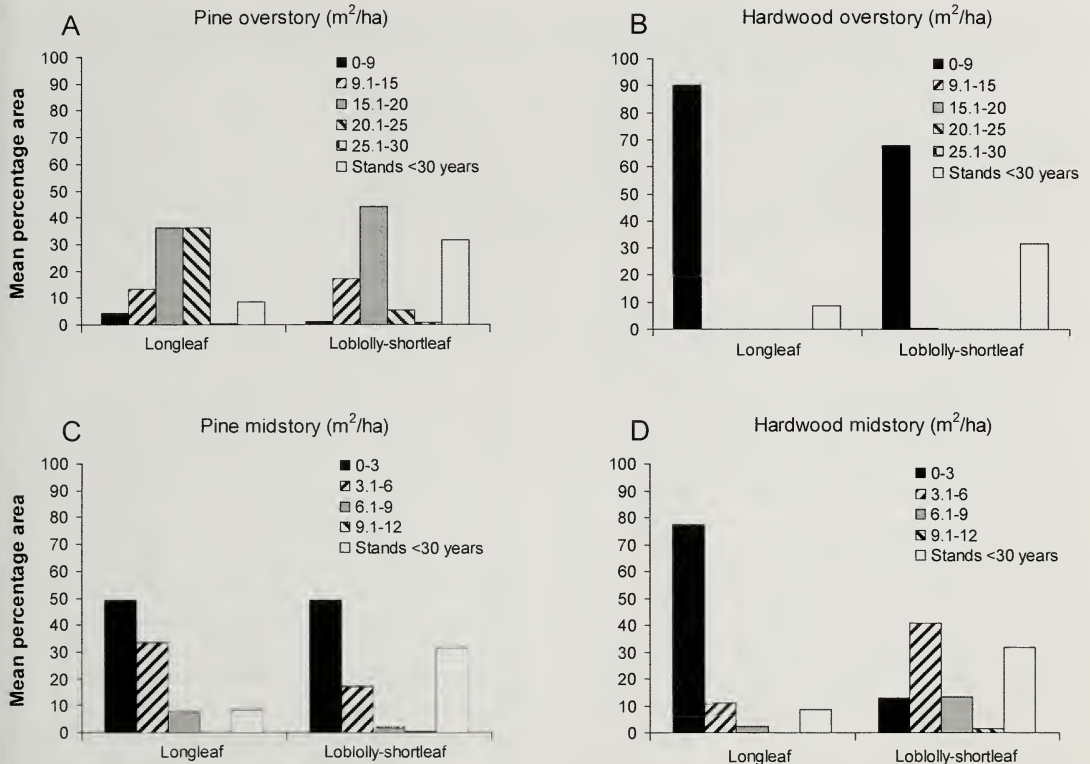


FIG. 2. Mean percentage of area within 800 m of Red-cockaded Woodpecker cavity-tree clusters occupied by each category of (A) pine overstory basal area, (B) hardwood overstory basal area, (C) pine midstory basal area, and (D) hardwood midstory basal area in longleaf pine ($n = 11$) and loblolly-shortleaf pine ($n = 13$) sites in eastern Texas, 1990–1991.

trees ($r = -0.60$, $P = 0.003$), and infested hectares ($r = -0.51$, $P = 0.016$) were negatively correlated with number of feeding trips per nestling. No significant correlations were found between indices of beetle abundance and the remaining reproductive and provisioning variables. At longleaf nests in which at least one fledgling was produced ($n = 15$), no significant correlations were found between indices of beetle abundance and any of the reproductive and provisioning variables.

Adult nutritional status.—Body mass was used to compare separately the nutritional status of adult male and female Red-cockaded Woodpeckers in longleaf and loblolly-shortleaf pine habitats. Body mass of adult males was significantly greater ($t = -2.25$, $P = 0.030$) in loblolly-shortleaf ($\bar{x} = 48.5$ g \pm 2.3 SD, $n = 27$) than in longleaf pine ($\bar{x} = 46.9$ g \pm 2.7 SD, $n = 18$). Adult females averaged only slightly heavier in loblolly-shortleaf ($\bar{x} = 46.6$ g \pm 2.2 SD, $n = 17$) than in longleaf

pine ($\bar{x} = 45.3$ g \pm 2.0 SD, $n = 13$), and the difference was not statistically significant ($t = -1.59$, $P = 0.12$).

DISCUSSION

Canopy trees in loblolly-shortleaf pine habitat were generally older, taller, and larger in diameter than in longleaf pine. Suitable mid-story conditions for Red-cockaded Woodpeckers were more widespread in longleaf than in loblolly-shortleaf pine. Soil-type differences and more effective prescribed burning in longleaf pine areas had a strong influence on differences in midstory condition between the two pine habitats (Conner and Rudolph 1989). Red-cockaded Woodpeckers are known to have an aversion to a well-developed stratum of midstory vegetation associated with both nesting (Conner and Rudolph 1989, Loeb et al. 1992) and foraging habitat (Rudolph et al. 2002; Walters et al. 2000, 2002). Thus, it might be expected that nest productivity of

TABLE 2. Southern pine beetle abundance (mean \pm SD) at longleaf ($n = 22$) and loblolly-shortleaf ($n = 25$) pine sites in eastern Texas during 1990 and 1991.^a

Variable	Longleaf	Loblolly-shortleaf	<i>t</i>	<i>P</i>
Number of beetle spots	0.32 \pm 0.57	2.80 \pm 2.80	4.33	<0.001
Number of infested trees	2.91 \pm 5.13	65.32 \pm 65.58	4.74	<0.001
Number of infested hectares	0.01 \pm 0.04	0.63 \pm 0.80	3.84	<0.001

^a The 2 years were not combined for southern pine beetle analyses due to the potential for substantial year-to-year changes in beetle abundance indices.

woodpeckers in habitat with an abundance of midstory vegetation (i.e., loblolly-shortleaf pine) would be lower than in longleaf pine.

Despite less suitable midstory conditions in loblolly-shortleaf pine habitat, woodpecker groups there performed at least as well reproductively as groups in longleaf pine, but only feeding trips per nest and relative prey biomass delivered to nestlings were significantly greater in the former. Our sample sizes were too small to detect biologically significant differences between pine habitats for the remaining reproductive and provisioning variables.

Helpers were more common in loblolly-shortleaf groups, but only once was there >1 per group. Other studies indicate that groups with helpers fledge significantly more young than groups without helpers (Lennartz et al. 1987, Walters 1990). In this study, increased group size did not significantly influence the number of feeding trips per nest even though helpers assisted with nestling provisioning. However, helpers may enhance reproductive success by assisting with incubation, brooding and feeding nestlings, territory defense, and defense against predators.

The relative biomass of arthropod prey delivered to nestlings was significantly greater in loblolly-shortleaf than longleaf pine habitat. At those loblolly-shortleaf sites where southern pine beetles were more abundant, adult Red-cockaded Woodpeckers made fewer feeding trips per nestling but delivered larger prey items. Access to larger prey items may benefit adults by reducing nestling provisioning effort.

The smallest mean for provisioned biomass per feeding trip (76.9 mg) for any nest in loblolly-shortleaf habitat was greater than that for 9 of the 15 nests in longleaf habitat. We know from field observations that adults from at least three of the six nests in longleaf habitat with large values for mean prey biomass per

feeding trip had access to one or more (exact number unknown) nearby dying pines. These trees were often loblolly pines located on wetter sites (i.e., streams or baygalls) within longleaf pine habitat, and were dying from either lightning strikes or southern pine beetle infestations. During provisioning observations, we noticed adults spending considerable time traveling between the direction of the dying pines and the nest. Thus, the high values of biomass provisioned to nestlings appear to be at least partially dependent on the local availability of dying pines that have an abundant supply of arthropod prey. A great number of arthropod species are attracted to such dying pines, which provide an abundance of food for Red-cockaded Woodpeckers (Ligon 1968, Hooper and Lennartz 1981, Conner et al. 2001).

Adult and larval southern pine beetles are fairly small prey items for Red-cockaded Woodpeckers. However, the adults and larvae of larger wood boring beetles (e.g., Cerambycidae and Buprestidae), which are attracted to pines infested by southern pine beetles, provide much larger prey items for foraging woodpeckers. Red-cockaded Woodpeckers have been observed to forage for as long as 55 min on small groups of dying pines infested with arthropods before moving on to a healthy tree (Schaefer 1996). Dying pines provide an important food source for Red-cockaded Woodpeckers throughout the year, particularly during the nesting season when young woodpeckers are being fed.

We suggest that the greater abundance of southern pine beetles in loblolly-shortleaf pine habitat and the resulting higher frequency of dying pines containing a diverse and abundant arthropod community are associated with elevated prey biomass. Dying pines were comparatively rare in longleaf pine habitat because this species is more resistant to southern

pine beetle infestation; this is due to its ability to produce copious amounts of resin and to the different physical properties of its resin (Hodges et al. 1979). Increased prey availability, in terms of biomass, is one indication of increased territory quality. Thus, the quality of foraging habitat at our loblolly-shortleaf pine study sites was greater than that at longleaf pine sites. That adult male Red-cockaded Woodpeckers weighed more in loblolly-shortleaf pine habitat suggests, at least in eastern Texas, that they are nutritionally more fit than those in longleaf pine habitat.

The abundant food source available to Red-cockaded Woodpeckers in dying pines is transient. During epidemic years southern pine beetles can devastate large areas of pine forest, including Red-cockaded Woodpecker foraging habitat and entire cavity-tree clusters. However, during non-epidemic years, when southern pine beetle attacks are confined to single trees or small groups of pines, prey availability may increase for Red-cockaded Woodpeckers. Territory quality influenced by the presence of ephemeral southern pine beetle infestations will fluctuate and can be unpredictable.

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EFFECTS OF NEST PREDATION AND BROOD PARASITISM ON POPULATION VIABILITY OF WILSON'S WARBLERS IN COASTAL CALIFORNIA

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ABSTRACT.—We studied the consequences of nest predation and brood parasitism on a population of Wilson's Warblers (*Wilsonia pusilla*) breeding in coastal riparian woodlands in northern California. We monitored 90 warbler nests from 1997 to 2000; only 16 of these produced Wilson's Warbler young. Of 74 failed nests, 73% (54/74) failed due to nest predation. Overall, 33% (30/90) of the nests were parasitized by Brown-headed Cowbirds (*Molothrus ater*). Nest success, as calculated by the Mayfield method, was 0.085 and notably lower than values reported for other warbler species. We used a simple demographic population model—under scenarios of high, average, and low productivity and survival—to evaluate the viability of this population and found it to be at risk of local extirpation without immigration. This was due to the combined effects of high levels of nest predation and the impacts of brood parasitism. Received 16 June 2003, accepted 6 April 2004.

Across their range, breeding populations of Wilson's Warbler (*Wilsonia pusilla*) have been declining at both regional and local scales over the past few decades (Ammon and Gilbert 1999, Sauer et al. 2001). According to Breeding Bird Survey data, Wilson's Warblers across the North American continent have been declining on average 2.0% per year during the period 1980 to 2000, and populations along the Pacific coast have been declining on average 1.8% per year over the same time period (Sauer et al. 2001). In contrast, data from a single site in coastal California indicate that the breeding population there is stable (Chase et al. 1997).

Population declines in breeding songbirds have been attributed to a variety of factors, including, but not limited to, loss, degradation, and fragmentation of habitat and associated factors that affect reproductive success and survival. There is evidence that the Wilson's Warbler population in coastal California is regulated primarily by breeding productivity (Chase et al. 1997); however, the factors that limit productivity are unknown. The leading causes of low reproductive success in songbirds are nest predation by vertebrate

predators and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*; Brittingham and Temple 1983; Martin 1992a, 1992b). High levels of nest predation and brood parasitism have been implicated in the decline of many songbird populations by directly affecting productivity and, ultimately, population dynamics (e.g., Pease and Grzybowski 1995).

While there have been few studies published documenting the breeding ecology and life history characteristics of western populations of Wilson's Warbler (Stewart 1973, Stewart et al. 1977, Ammon and Gilbert 1999), little work has been done to explore causes of recent declines and, more specifically, factors limiting reproductive success. Population declines in the past have been attributed to loss and degradation of riparian breeding habitat (Ammon and Gilbert 1999). However, few estimates of reproductive success exist and, to our knowledge, no Mayfield (1975) estimates of nest success have been reported. There are even fewer accounts of cowbird parasitism and its effects on reproductive success of Wilson's Warblers.

In this study, we report on the breeding biology and population viability of a coastal population of Wilson's Warblers breeding in Marin County, California. Our objectives were to (1) examine the effects of cowbird parasitism and nest predation on warbler reproductive success, and (2) develop a simple demographic population model to assess the viability of this local population.

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METHODS

Study areas.—Our study was conducted in the Golden Gate National Recreation Area (GGNRA) in coastal Marin County, California, just north of the San Francisco Bay area. Fieldwork occurred from mid-April to early August 1997 to 2000 along two riparian woodlands, Lagunitas Creek (38° 02' N, 122° 45' W) and Redwood Creek (37° 51' N, 122° 34' W). The Lagunitas Creek site contained two plots and the Redwood Creek site three, including Muir Beach. Nest monitoring at Muir Beach was conducted only from 1997 to 1999. Each study plot was approximately 3.6 ha in size.

All study sites were similar in vegetation type and typical of riparian communities in the surrounding area. Red alder (*Alnus rubra*) and willow (*Salix* spp.) dominated the sites with lesser amounts of box elder (*Acer negundo*), California bay (*Umbellularia californica*), California buckeye (*Aesculus californica*), and coast live oak (*Quercus agrifolia*). Understory species consisted primarily of California blackberry (*Rubus ursinus*), Himalayan blackberry (*R. discolor*), poison oak (*Toxicodendron diversilobum*), and fern species.

The areas surrounding the study sites were largely oak-bay woodlands and coastal scrub. At Lagunitas Creek, there was light livestock grazing in fields adjacent to the creek and our plots. We chose to treat the Muir Beach plot separately (even though it is part of Redwood Creek) because (1) it is divided by a road; (2) there is a residential community (~150 homes), small horse stable, and a tavern immediately adjacent; (3) there is a public picnic area and 175-car parking lot within and adjacent; (4) it is a heavily used recreational area with over 400,000 visitors per year (National Park Service unpubl. data); and (5) it is the only plot where unsupervised domestic dogs (*Canis domesticus*) and cats (*Felis domesticus*) were seen.

Nest searching and monitoring.—Wilson's Warbler nests were located and monitored using guidelines described by Martin and Geupel (1993). We located nests by observing parental behavior and systematically searching the vegetation. Nests were monitored every 1–4 days until nest failure or fledging. A nest was considered successful if it fledged at least

one warbler young. Fledging was assigned based on the condition of the nest (e.g., matted rim and/or fecal matter and no signs of depredation, stage of the nesting cycle), and/or evidence of fledglings within close proximity of the nest near the expected fledging date. We considered a nest to have failed if it was abandoned or depredated (disappearance of nest contents) prior to the expected fledging date.

Nests were considered parasitized if at any stage in the nesting cycle they contained a cowbird egg or nestling. We considered nests to have failed from cowbird parasitism if only cowbird eggs or nestlings were observed in the nest during all observations, nests were abandoned during egg laying and cowbird eggs were present, or if only cowbird eggs or nestlings were present in the nest after warbler eggs or young were observed. Parasitized nests were considered successful if warbler young fledged from the nest.

Reproductive success.—Nest survival probabilities were calculated using the Mayfield (1975) method with the standard error estimator developed by Johnson (1979). The Mayfield method is based on nest losses divided by the total number of days nests were observed and, thus, at risk of failure. Survival probabilities were calculated for each stage of nesting (egg laying, incubation, and nestling) and for the entire nesting period. Estimates were based on a 26-day nesting period (4 egg-laying days, 12 incubation days, and 10 nestling days) as determined by our nest monitoring data. When calculating "exposure" days (the total number of observation days) for nests with known fates, we used the midpoint between the last observed active date and the first observed inactive date; for nests with unknown fates, the last active date was used for counting exposure days (Last-Active B method in Manolis et al. 2000). We compared differences in nest success probabilities among nesting stages, study sites, and between parasitized and unparasitized nests with Program CONTRAST (Sauer and Williams 1989).

We also calculated the following components of reproductive success: clutch size, clutch-initiation date, hatching success, nestling number, fledging success, and fledgling number. These were calculated for both cowbirds and warblers separately, with the exception of clutch initiation. Clutch size was based

on the maximum number of eggs present throughout egg laying. Clutch-initiation dates were estimated based on the first egg laid for a nesting attempt or backdated to calculate when the first egg was laid. Hatching and fledging success were defined as the total number of nestlings and fledglings, respectively, divided by clutch size. The maximum number of young observed between hatching and fledging was the nestling number. Fledgling number was based on the number of nestlings seen during the last nest check prior to the estimated fledging date for successful nests. Comparisons between parasitized and unparasitized nests were made for all components of reproductive success.

Population trajectory.—To evaluate population viability, we developed a simple demographic population model following Pulliam (1988) and Donovan et al. (1995). We calculated lambda (λ) values using the following equation:

$$\lambda = P_A + P_J B$$

where λ is the finite rate of increase, P_A represents adult survival, P_J represents juvenile survival from fledging to the first breeding season, and B is a measure of productivity representing the number of female offspring produced per year. This last component is composed of three sub-components: the number of nesting attempts \times probability a nesting attempt is successful \times number of female young produced per successful nest; the second sub-component incorporates our Mayfield estimates of nest success. $P_J B$ is a measure of recruitment rate based on the number of new female recruits produced per year.

Under this model, which calculates a finite (annual) rate of increase, the population is considered a sink ($\lambda < 1$) if juvenile recruitment is less than adult mortality. Conversely, if juvenile recruitment (i.e., $P_J B$) is greater than adult mortality it is considered a source ($\lambda > 1$), and if the two are equivalent the population is stable ($\lambda = 1$; Pulliam 1988). For our calculations, we used $P_A = 0.503$ (± 0.035 SE, 95% CI = 0.435–0.571), the adult survival estimate from coastal Marin County (Chase et al. 1997). Because direct estimates of juvenile survival are largely unknown (Gardali et al. 2003), we used a conservative estimate of juvenile survival and assumed it was

70% that of adults (0.352; Powell et al. 1999, Perkins and Vickery 2001). Based on our field data, the number of female offspring per successful nest was 1.7. The formula was evaluated using two, three, and four nesting attempts due to the variability of the number of nesting attempts per season across the warblers' range (Ammon and Gilbert 1999). Additionally, we used our overall nest survival estimate and its 95% confidence interval, and juvenile and adult annual survival to evaluate the population under the observed average, best-, and worst-case scenarios.

Statistical analysis.—Nominal logistic regression was used to test for differences in predation and parasitism frequency between sites (Nur et al. 1999). Comparisons of predation rates and nest abandonment between parasitized and unparasitized nests were made using the Pearson chi-square test. We used ordinal logistic regression to determine whether clutch size, hatching success, nestling number, fledging success, and fledgling number were significantly different between parasitized and unparasitized nests. Due to small sample size, data were combined across years and we excluded those nests that were abandoned or depredated prior to the end of egg laying ($n = 14$). All statistical analyses were performed using JMP software (Sall and Lehman 1996) and means are presented as \pm SE.

RESULTS

We located and monitored 90 Wilson's Warbler nests over the course of our study. The earliest nest initiation date (first egg laid) was 17 April, and the last was 10 July. Most nests (68%) were built in blackberry shrubs, 18% in ferns, and 12% in eight other plant species. Mean nest height was 50.4 ± 2.5 cm. Only 16 nests were successful (18%) and 74 (82%) failed to produce young (Table 1).

Causes of nest failure.—Nest predation was responsible for more nest failures than failure caused by cowbird parasitism, 73.0% (54/74) versus 13.5% (10/74), respectively. Of 54 depredated nests, 48 were completely depredated, resulting in the loss of the entire clutch or brood, and 6 were partially depredated and subsequently abandoned. The remaining nests were abandoned due to unknown causes ($n = 6$), failed due to weather ($n = 3$), or were accidentally destroyed ($n = 1$). Of the 10 nests

TABLE 1. Nest outcome and causes of failure for Wilson's Warblers breeding in coastal Marin County, California, 1997–2000. BHCO refers to Brown-headed Cowbird parasitism.

	All nests	Parasitized nests	Unparasitized nests
Nest outcome			
Total number of nests	90	30	60
Successful ^a	16	1	15
Unsuccessful	74	29	45
Percent successful	18%	3%	25%
Causes of nest failure			
Depredated ^b	54	18	36
BHCO ^c	10	10	—
Abandoned (unknown)	6	—	6
Abandoned (weather)	3	1	2
Abandoned (other)	1	—	1

^a Nests from which at least one warbler fledged.

^b Includes four nest failures due to parasitism and subsequent depredation.

^c Includes four nests fledging BHCO, four lost to predation, and two abandoned.

that failed due to cowbird parasitism, four fledged cowbird young, four were subsequently depredated, and two were abandoned (Table 1).

Nest predation differed among sites for all years combined ($\chi^2 = 6.58$, $df = 2$, $P = 0.043$). Predation rates were highest at Muir Beach (91.7%), and lower at Lagunitas Creek (54.5%) and Redwood Creek (61.8%; Table 2). The frequency of predation did not differ between parasitized (73%) and unparasitized (60%) nests ($\chi^2 = 1.55$, $df = 1$, $P = 0.21$). Likewise, there was no difference in the frequency of nest abandonment for parasitized (25%) and unparasitized (75%) nests ($\chi^2 = 0.27$, $df = 1$, $P = 0.60$).

Brood parasitism.—Cowbirds parasitized

TABLE 2. Frequency of nest predation and cowbird parasitism observed in Wilson's Warblers at three sites in coastal Marin County, California, 1997–2000.

Site	Nest predation		Parasitism	
	%	<i>n</i>	%	<i>n</i>
Lagunitas Creek (<i>n</i> = 44)	54.5	24	25.0	11
Muir Beach (<i>n</i> = 12)	91.7	11	83.3	10
Redwood Creek (<i>n</i> = 34)	61.8	21	26.5	9
All sites (<i>n</i> = 90)	62.2	56	33.3	30

33.3% (30/90) of all nests, 3% (1/30) of which were successful, as compared to 25% (15/60) of unparasitized nests. The frequency of parasitism (all years combined) was greater at Muir Beach (83.3%) than at Lagunitas Creek (25.0%) and Redwood Creek (26.5%; $\chi^2 = 14.97$, $df = 2$, $P < 0.001$; Table 2). Of the 30 parasitized nests, 26 contained one cowbird egg and 4 had two cowbird eggs. The mean number of cowbird eggs and nestlings per parasitized nest was 1.16 ± 0.07 and 0.77 ± 0.12 , respectively (Table 3). At least one cowbird fledged from each of four parasitized nests, and two cowbirds fledged from one nest, for an overall mean of 0.22 ± 0.10 cowbirds fledged per parasitized nest (Table 3). Warbler young fledged from only one parasitized nest. An inactive nest was parasitized after being depredated.

Clutches in parasitized nests contained fewer warbler eggs (1.52 fewer) than unparasitized nests ($\chi^2 = 43.13$, $df = 1$, $P < 0.001$; Table 3). Moreover, the percent of warbler eggs that hatched was lower in parasitized nests (35.7%) than in unparasitized nests (63.8%; $\chi^2 = 5.55$, $df = 1$, $P = 0.019$; Table 3) and we found fewer warbler nestlings in

TABLE 3. Five estimates of reproductive success for parasitized and unparasitized Wilson's Warbler nests (mean \pm SE), coastal Marin County, California, 1997–2000.

	Wilson's Warbler			
	Parasitized nests	Unparasitized nests	Combined	Cowbird
Clutch size	1.96 \pm 0.16	3.48 \pm 0.12	2.92 \pm 0.13	1.16 \pm 0.07
Hatching success ^a	0.36 \pm 0.09	0.64 \pm 0.07	0.53 \pm 0.06	0.64 \pm 0.09
Number of nestlings	0.71 \pm 0.19	2.31 \pm 0.26	1.72 \pm 0.20	0.77 \pm 0.12
Fledging success ^b	0.04 \pm 0.04	0.28 \pm 0.06	0.19 \pm 0.04	0.18 \pm 0.08
Number of fledglings	0.11 \pm 0.11	1.06 \pm 0.25	0.71 \pm 0.17	0.22 \pm 0.10

^a Hatching success: total number of nestlings/clutch size.

^b Fledging success: total number of fledglings/clutch size.

TABLE 4. Daily survival and total nest success (Mayfield 1975) for Wilson's Warblers breeding in riparian woodlands, coastal Marin County, California, 1997–2000.

	Number of nests	Exposure days	Losses	Daily survival (SE, 95% CI)	Nest success (95% CI)
Lagunitas Creek	44	436	30	0.931 (0.012, 0.907–0.955)	0.157 (0.080–0.302)
Muir Beach	12	95	12	0.874 (0.034, 0.807–0.940)	0.030 (0.004–0.203)
Redwood Creek	34	219	24	0.890 (0.021, 0.859–0.932)	0.049 (0.014–0.159)
All sites	90	731	66	0.910 (0.011, 0.889–0.930)	0.085 (0.047–0.154)

parasitized nests ($\chi^2 = 14.76$, $df = 1$, $P = 0.001$). Similarly, fledging success differed between parasitized (3.6%) and unparasitized (27.6%) nests ($\chi^2 = 8.79$, $df = 1$, $P = 0.003$; Table 3) and parasitized nests fledged fewer warbler young than unparasitized nests ($\chi^2 = 9.27$, $df = 1$, $P = 0.002$). Parasitized and unparasitized nests averaged 0.71 ± 0.19 and 2.31 ± 0.26 nestlings, respectively.

Daily survival and nest success.—The Mayfield (1975) estimate of nest success was 8.5% (95% CI = 0.047–0.154; Table 4). Differences among sites in daily survival rates were marginally significant ($\chi^2 = 4.72$, $df = 2$, $P = 0.094$; Table 4). Daily survival rates of parasitized and unparasitized nests did not differ ($\chi^2 = 1.54$, $df = 1$, $P = 0.21$). Daily survival was lowest during the nestling stage (0.87 ± 0.022), and slightly greater during egg laying (0.93 ± 0.023) and incubation (0.93 ± 0.013 ; $\chi^2 = 5.88$, $df = 2$, $P = 0.053$).

Population trajectory.—The demographic population model suggests that this population of Wilson's Warbler is not self-sustaining in the absence of immigration from other populations. We used a value of 1.7 female offspring per successful nest (based on our field

data) and evaluated the model under a variety of scenarios. Using conservative estimates of survival and productivity and two nesting attempts, $\lambda = 0.46$ (Table 5). When intermediate estimates of survival and productivity for birds attempting three nests per season were used, $\lambda = 0.62$ (Table 5). Under the best-case scenario (high survival and productivity, four nesting attempts per season), $\lambda = 0.98$ and approaches the value (1) required for a stable population.

DISCUSSION

Nest success in this study was extremely low. The proportion of successful nests (0.18) was slightly greater than that reported from inner-coastal California (0.16) and far lower than eight other estimates (0.33–0.93; summarized by Ammon and Gilbert 1999).

Since no Mayfield (1975) estimates of nest survival exist for the Wilson's Warbler, we were unable to compare our survival estimates to those of previous studies. While estimates of nest success may be variable across habitat types, years, and between species, our estimates were notably lower than those reported for other warbler species. For example, May-

TABLE 5. Lambda values (finite rate of increase) for population models using mean and 95% confidence intervals for survival and productivity (i.e., low, mean, and high productivity and survival) with two, three, and four nesting attempts for Wilson's Warbler, coastal Marin County, California, 1997–2000. Number of female offspring/successful nest set at 1.7 (see text).

Number of nesting attempts	Low productivity ^a (lower CI)			Mean productivity ^b			High productivity ^c (upper CI)		
	2	3	4	2	3	4	2	3	4
Low survival ^d (lower CI)	0.46	0.47	0.49	0.50	0.53	0.57	0.59	0.67	0.75
Mean survival ^e	0.53	0.55	0.56	0.58	0.62	0.66	0.68	0.77	0.87
High survival ^f (upper CI)	0.60	0.62	0.64	0.66	0.70	0.75	0.78	0.88	0.98

^a Low productivity: Mayfield success = 0.047.

^b Mean productivity: Mayfield success = 0.085.

^c High productivity: Mayfield success = 0.154.

^d Adult survival = 0.435, juvenile survival = 0.305.

^e Adult survival = 0.503, juvenile survival = 0.352.

^f Adult survival = 0.571, juvenile survival = 0.400.

field (1975) estimates for the Worm-eating Warbler (*Helmitheros vermivorus*) range from 0.37 to 0.50 in Virginia (Dececco et al. 2000), 0.44 for the Hooded Warbler (*Wilsonia citrina*) in South Carolina (Moorman et al. 2002), and 0.50 for Orange-crowned Warbler (*Vermivora celata*) and 0.58 for Virginia's Warbler (*V. virginiae*) in Arizona (Martin 1992a). The lowest estimate for any warbler (summarized by Martin 1992a) is 0.20 for the Kirtland's Warbler (*Dendroica kirtlandii*).

Predation appeared to be the primary cause of nest failure for Wilson's Warblers breeding in coastal riparian woodlands in Marin County. However, we documented a relatively high rate of brood parasitism and believe that the combined effects of parasitism and predation explain the poor reproductive success. For example, the difference in nestling number between parasitized and unparasitized nests was large and contributed to reduced reproductive success. Our results are similar to those of other studies in that they point to nest predation and brood parasitism as the leading causes of nesting failures in songbird populations (reviewed by Martin 1992a).

While predation and parasitism were high at all study sites, they were significantly greater at Muir Beach than at the other sites. Although our sample size of nests at Muir Beach was low, we suspect that the higher levels of predation and parasitism at that site may have resulted from the nests' close proximity to a public picnic area, a horse stable, and a small residential community. Predator densities and predation pressure are higher in areas near suburban landscapes (Wilcove 1985, Andr en 1992). At Muir Beach, it is likely that several native and non-native predators are in greater abundance than at our other sites. For example, house cats were only observed at Muir Beach, and several corvid species frequent the picnic area and, perhaps, the nearby bird feeders. Additionally, raccoons (*Procyon lotor*) may have been more abundant at Muir beach, as they are commonly known to forage from trash cans. In addition, cowbirds may have benefited from the horse pasture, feeders, and mowed picnic area at Muir Beach.

We observed significantly lower reproductive success in warbler nests parasitized by cowbirds. Clutch sizes in parasitized nests were smaller, probably the result of egg-re-

moval behavior by female cowbirds, as were hatching and fledging success. In general, parasitized nests failed entirely. We observed only one instance of warbler young fledging from a parasitized nest.

Brown-headed Cowbirds experienced poor reproductive success in Wilson's Warbler nests due to high rates of nest predation; cowbird fledging success was notably lower than that reported for several other species of cowbird hosts (reviewed by Ortega 1998), suggesting that warblers in this region may not be optimal cowbird hosts.

The Wilson's Warbler is considered an uncommon cowbird host (Ammon and Gilbert 1999), yet it was one of the most common host species at our study sites (Point Reyes Bird Observatory unpubl. data). The proportion of nests parasitized in our study (33%), together with estimates for Santa Barbara and San Luis Obispo counties, California (55%, $n = 11$; Friedmann et al. 1977), suggest that Wilson's Warbler is a common cowbird host in coastal California.

High levels of nest predation combined with brood parasitism are adversely affecting this population of Wilson's Warbler. Based on our demographic population model, this local population constitutes a sink; efforts to identify source populations within the region are needed to determine whether the regional population can be sustained. High levels of nest predation combined with the effects of brood parasitism point to the underlying causes of recent population declines. Low reproductive success appears to be associated with the proximity of nesting sites to human habitation (i.e., our Muir Beach site), although success was poor at all of our sites. Nest-monitoring data from other sites in coastal California are needed to understand the metapopulation dynamics of this species. Wilson's Warblers are not restricted to riparian habitats in coastal Marin County and studies that compare reproductive success among different habitats (e.g., riparian versus coniferous forest) would be useful.

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SPATIAL FORAGING DIFFERENCES IN AMERICAN REDSTARTS ALONG THE SHORELINE OF NORTHERN LAKE HURON DURING SPRING MIGRATION

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ABSTRACT.—Lowland coniferous forests adjacent to northern Lake Huron provide important stopover habitat for landbirds during spring migration. Large numbers of aquatic insects emerging from nearshore waters of northern Lake Huron appear to be an important food source. In this study we compared the foraging behavior of a long-distance landbird migrant, the American Redstart (*Setophaga ruticilla*), in areas with high densities of emergent aquatic insects to areas with few or no emergent aquatic insects to assess the significance of these arthropods as an early spring food source. Redstarts foraged differently in shoreline habitats relative to inland habitats of similar vegetation composition. Both males and females gleaned significantly more in shoreline habitats as compared to inland areas of similar vegetation composition, and inland birds performed more sally strikes than birds at the shoreline. Both sexes also varied the use of tree species in which they foraged. Redstarts used northern white cedar (*Thuja occidentalis*) more at shoreline than inland, while inland redstarts foraged in deciduous trees more than at the shoreline. We suggest that differences in foraging between shoreline and inland locations were responses to differences in prey types and abundance, most notably the presence of emergent aquatic insects (Diptera: Chironomidae) in shoreline habitat. Our results complement those of previous work, suggesting that midges provide a critical early season resource for landbirds migrating through Michigan's eastern Upper Peninsula during spring. Received 30 September 2003, accepted 26 March 2004.

During spring and early summer in temperate North America, large numbers of aquatic insects that have metamorphosed into sexually mature adults often amass in terrestrial habitats adjacent to riparian and lacustrine systems (Armitage 1995, McCafferty 1998). These invertebrates are relatively weak fliers (e.g., Kovats et al. 1996) and tend to be restricted to nearshore terrestrial habitats. In Michigan's eastern Upper Peninsula, midges (Diptera: Chironomidae) are the predominant aquatic arthropods when migratory landbirds stop during spring migration. These invertebrates swarm profusely in shoreline areas while being virtually nonexistent inland (DNE unpubl. data).

Recent evidence suggests that lowland coniferous forests adjacent to northern Lake Huron provide important stopover habitat for spring migrants. More landbirds are found in

nearshore, midge-abundant habitats than inland habitats with comparable vegetation (DNE unpubl. data). Further, Black-throated Green Warblers (*Dendroica virens*) forage in and use habitat elements differently in midge-abundant habitats compared to inland, midge-depauperate habitats (Smith et al. 1998), and American Redstarts (*Setophaga ruticilla*) and Black-throated Green Warblers forage at higher rates in midge-abundant areas relative to habitats with no midges (Seefeldt 1997).

Here we describe shoreline/inland differences in the foraging behavior of a long-distance landbird migrant, the American Redstart, during spring migration in Michigan's eastern Upper Peninsula. By focusing on spring migration, we were able to examine bird behavior when shoreline/inland differences in arthropod abundances were most dramatic (Smith et al. 1998; DNE unpubl. data). We compared redstart foraging behavior in areas with high densities of midges to areas with few or no emergent midges to assess the significance of these arthropods as a food source during early spring.

METHODS

Study area.—The study area included approximately 80 km of shoreline, extending

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from Horseshoe Bay to DeTour State Park in Mackinac and Chippewa counties, respectively (45° 57' to 46° 04' N, 84° 00' W to 84° 44' W). Limestone and dolomite peninsulas define much of the shoreline, with sandy coves and marshes characterizing borders of intervening bays. Conifers, especially northern white cedar (*Thuja occidentalis*), balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), eastern white pine (*Pinus strobus*), and deciduous species, including paper birch (*Betula papyrifera*), and quaking aspen (*Populus tremuloides*), dominate the forest. Forest composition was relatively uniform throughout the study area, as determined by vegetation sampling performed in association with a bird census project that occurred in the same landscape (Smith et al. 1998; DNE unpubl. data). Using the point-centered technique of Cottam and Curtis (1956), DNE (unpubl. data) determined forest composition at 45 permanent, 50-m fixed-radius bird census points positioned on nine transects spaced uniformly across the study area. Sample points were positioned at 0, 0.4, 0.8, 1.6, and 3.2 km from the lake-shore. Canopy height ranged from 10 to 15 m. The understory was heavily browsed by white-tailed deer (*Odocoileus virginianus*) and consisted mostly of balsam fir and white spruce.

Foraging observations.—We collected data on foraging American Redstarts during spring migration of 1993 and 1994. To avoid bias in our sampling effort, we spent equal amounts of time in shoreline and inland habitats while searching for foraging redstarts. Observations of spring migrants commenced when the first birds arrived in early May and continued through early June, the onset of breeding for birds in the area (Wood 1951; DNE and MJH pers. obs.; R. J. Smith and F. R. Moore unpubl. data). To compare foraging at shoreline and inland locations, observations made ≤ 0.4 km from Lake Huron were designated as shoreline, and observations made 0.4–3.2 km from the lake were designated as inland. We selected 0.4 km as the boundary between shoreline and inland because midge abundance drops precipitously beyond this point (DNE unpubl. data).

We used the protocol of Hejl et al. (1990) to minimize the likelihood of pseudoreplication. Only the first bird (of each sex) detected

in a flock was used as a subject. We recorded additional data only after an observer had traveled ≥ 30 m or ≥ 10 min had elapsed since the previous observation. To reduce discovery bias, we waited 5 sec after making initial visual contact, and then recorded the subsequent foraging maneuver performed by the bird (Morrison 1984, Hejl et al. 1990).

Foraging maneuvers were categorized as (1) glean, a maneuver directed at a prey item on a substrate while the bird was either perched or hopping; (2) sally hover, a maneuver in which a stationary prey item on a substrate is attacked by a hovering bird; and (3) sally strike, a maneuver in which both the insect and bird are in flight—also known as fly-catching or hawking behavior (Sabo 1980, Petit et al. 1990a).

We described the location of a foraging maneuver both horizontally and vertically within a tree. To characterize horizontal position, we arbitrarily divided a tree into inner, middle, and outer thirds (MacArthur 1958, Remsen and Robinson 1990). We also recorded foraging height for each bout by using a clinometer to measure the angle from observer to the bird and an optical rangefinder to measure distance; these data were converted to height (m) using the appropriate trigonometric equation. At the end of each observation we also recorded the species of tree in which the bird was observed, time of day, distance from the shoreline, and weather conditions.

We pooled data across years to maximize sample sizes. Only the five most frequently used tree species were considered when analyzing tree species used during foraging: white spruce, balsam fir, northern white cedar, quaking aspen, and paper birch. All data were analyzed using SPSS (2000). Treatment of variables depended upon whether data were continuous or categorical (Zar 1996). We used a General Linear Model to resolve differences in foraging height by sex and observation location (shoreline versus inland). Log-likelihood ratio (G) tests were used to analyze frequency data such as spatial differences in use of tree species, maneuver used, and horizontal position while foraging. Log-likelihood ratio (G) tests also were used to compare actual to expected use of northern white cedar by foraging redstarts. If redstarts preferred to forage in (or avoided) cedar, then they would exhibit

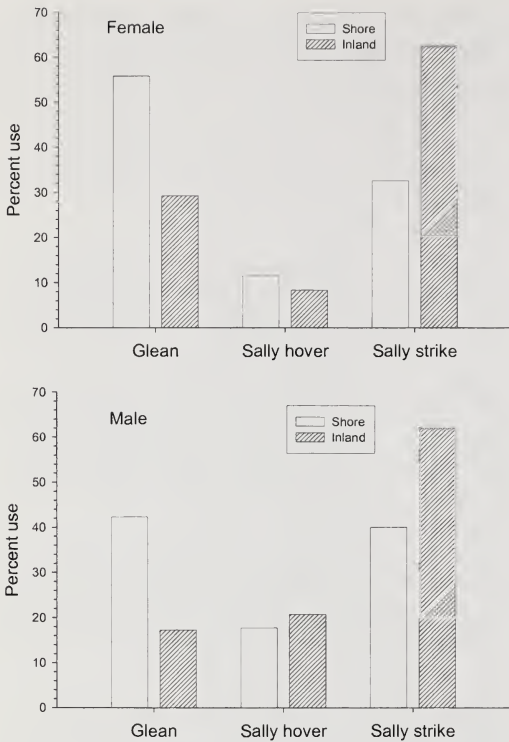


FIG. 1. Comparison of American Redstart foraging maneuvers at shoreline and inland habitats during spring migration 1993–1994, northern Lake Huron, Michigan (female $n = 67$, male $n = 379$).

a disproportionate use of cedar (Morrison et al. 1998). We used relative density estimates of cedar—calculated from vegetation sampling—to derive expected redstart use of cedar. Statistical significance was accepted at $P \leq 0.05$.

RESULTS

Males did not differ by age in foraging maneuvers used ($G = 4.89$, $df = 2$, $P = 0.087$, $n = 283$), nor did males differ from females in their use of foraging maneuvers ($G = 3.32$, $df = 2$, $P = 0.19$, $n = 333$). The type of foraging maneuver used, however, was dependent on habitat for both males ($G = 6.24$, $df = 2$, $P = 0.044$, $n = 379$) and females ($G = 6.22$, $df = 2$, $P = 0.045$, $n = 67$). Both sexes gleaned more at shoreline than inland locations (males: 42 versus 18%; females: 56 versus 29%) and used more sally strikes inland than at the shoreline (males: 64 versus 40%; females: 63 versus 32%; Fig. 1).

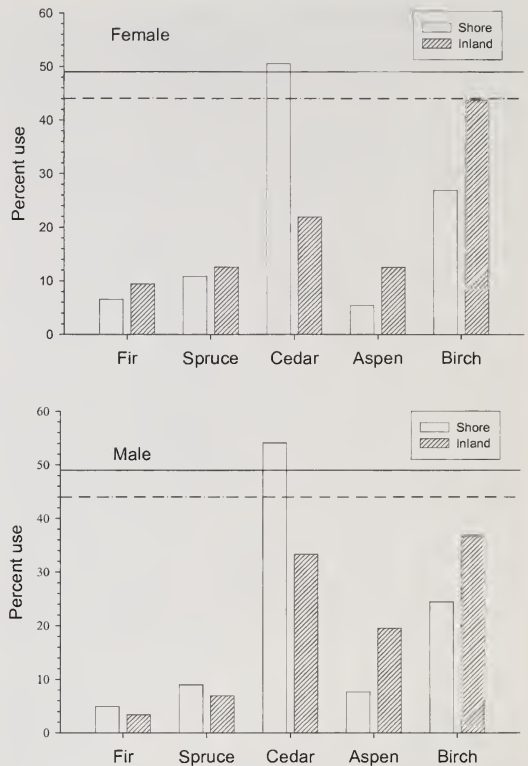


FIG. 2. American Redstart tree use in shoreline and inland habitats during spring migration 1993–1994, northern Lake Huron, Michigan (female shoreline $n = 93$, female inland $n = 32$; male shoreline $n = 590$, male inland $n = 87$). The solid reference line indicates relative density of northern white cedar in shoreline habitats and the dashed line indicates relative density of cedar inland.

There was no relationship between tree species selected for foraging and age of males ($G = 4.85$, $df = 4$, $P = 0.30$, $n = 229$) or gender ($G = 4.35$, $df = 4$, $P = 0.36$, $n = 363$). Males used tree species for foraging differently in shoreline habitats as compared to inland ($G = 21.23$, $df = 4$, $P < 0.001$, $n = 677$); the relationship was not significant in females ($G = 9.06$, $df = 4$, $P = 0.060$, $n = 125$). In shoreline habitats, both males and females foraged more in northern white cedar than in other tree species (males 55%, females 52%), but they were observed more in aspen and birch inland relative to the shoreline (Fig. 2). Redstarts foraging in shoreline habitats did not use northern white cedar disproportionately (male: $G = 0.16$, $df = 1$, $P = 0.66$, $n = 590$; female: G

= 0.033, $df = 1$, $P = 0.81$, $n = 93$), but inland they did use cedar significantly less than expected (male: $G = 4.54$, $df = 1$, $P = 0.038$, $n = 87$; female: $G = 4.33$, $df = 1$, $P = 0.042$, $n = 32$; Fig. 2).

Foraging height was not related to male age ($F_{1,374} = 2.60$, $P = 0.11$), and male foraging height did not differ between shoreline and inland habitats ($F_{1,374} = 0.02$, $P = 0.89$); there was no male age by habitat interaction for foraging height ($F_{1,374} = 0.14$, $P = 0.71$). Foraging height of the sexes did not differ ($F_{1,441} = 2.27$, $P = 0.13$), nor did foraging height differ between shoreline and inland habitats ($F_{1,441} = 0.24$, $P = 0.63$); there was no sex by habitat interaction for foraging height ($F_{1,441} = 0.01$, $P = 0.99$). We found no shoreline/inland differences in horizontal position of males and females within trees (male: $G = 2.16$, $df = 2$, $P = 0.34$, $n = 378$; female: $G = 0.36$, $df = 2$, $P = 0.84$, $n = 67$).

DISCUSSION

Landbirds are known to vary their foraging in response to a number of factors, including structural differences in habitat (Collins 1983, Holmes and Schultz 1988), inter- and intra-specific competition (Rappole and Warner 1976, Laursen 1978, Morse 1980), including gender (Morse 1968, Holmes 1986, Ornat and Greenberg 1990, Petit et al. 1990b) and age (Woodrey 1995) interactions, weather (Pinkowski 1977), ambient temperature (Ford et al. 1990), thermoregulatory requirements (Martin and Karr 1990), and distribution, diversity and abundance of prey species (Holmes and Schultz 1988, Ford et al. 1990, Szaro et al. 1990, Smith et al. 1998). While the observed shoreline/inland differences in redstart foraging might be attributable to one or more of these factors, our results most likely reflect shoreline/inland differences in the abundance and activity of arthropods.

The observed variation in redstart foraging is likely not a consequence of differences in forest composition because our equal sampling effort, distributed across such a large landscape, should have eliminated any spurious effects between shoreline and inland. Moreover, vegetation sampling performed at the same scale as behavior sampling indicated little shoreline/inland difference in density of

tree species throughout our study area (Smith et al. 1998; DNE unpubl. data).

It is possible that differences in migrant densities between shoreline and inland (DNE unpubl. data) may have caused birds to vary their foraging by creating a situation in which shoreline birds experienced enhanced competition. Consequently, migrants in shoreline locations may have altered their foraging relative to those inland as they sought to alleviate enhanced competition associated with higher numbers of competitors. While our data are insufficient to rule this out, we point out that the shoreline/inland differences observed in redstarts were very similar to foraging differences previously documented in Black-throated Green Warblers (Smith et al. 1998). As with redstarts, during spring migration Black-throated Green Warblers gleaned more at the shoreline while exhibiting more sally hovers and sally strikes inland. Furthermore, Black-throated Green Warblers foraging in shoreline locations used cedar more than other tree species, while birds observed inland dramatically reduced their use of cedar, instead foraging more in deciduous species such as paper birch and quaking aspen.

Differential distribution by age or sex also could have influenced foraging, if there were age or sex differences in how redstarts foraged at our site. Age- and/or sex-mediated habitat segregation has been demonstrated among redstarts on the wintering grounds (Marra et al. 1993, Parrish and Sherry 1994), during migration (Woodrey 1995), and during the breeding season (Sherry and Holmes 1997). However, we found no age or gender effect in how birds foraged or used tree species.

There were obvious microclimate differences between shoreline and inland areas within our study site (DNE unpubl. data). Shoreline habitats were, on average, cooler and remained cooler longer. Redstarts may have varied foraging in response to these temperature differences. Martin and Karr (1990) found that a number of warbler species increased flying maneuvers during the colder periods of early spring and late fall migration. They suggested that use of aerial maneuvers during cold periods may be more efficient than nonflying maneuvers because of increased heat production by flight muscles. However, we found that redstarts performed more nonflying ma-

neuers (gleans) in cooler shoreline habitats and more aerial maneuvers (sally hovers and sally strikes) in warmer, inland areas. These results are contrary to what would be expected if birds increased aerial maneuvers to enhance thermoregulatory efficiency, but they correspond with expectations if birds were responding to increased activity of flying invertebrates in warmer habitats (see below).

The Great Lakes' influence on local climate, vegetation, and animal communities is especially apparent in nearshore terrestrial habitats (Eichenlaub 1979). Temperature depression resulting from onshore winds delays the phenological development of vegetation (Albert et al. 1986; DNE unpubl. data) and presumably the emergence and activity of arthropods, as both are dependent upon ambient air temperature (Williams 1961). Shoreline microclimate differs from inland and likely results in unique abundance and distribution patterns of arthropods.

Evidence for differences in arthropod abundance between shoreline and inland areas is suggested by differing foraging maneuvers in the two areas. Inland, away from the cooling influence of the lake, redstarts performed more sally strikes and fewer substrate-directed gleanings. Black-throated Green Warblers also increased their use of sally strikes at inland sites in Michigan's eastern Upper Peninsula (Smith et al. 1998). Increases in aerial maneuvers such as sally strikes suggest that either flying insects were more abundant inland, flying insects were more active inland, or some combination of the two. Because of the influence of temperature on invertebrate development and activity, any temperature differential between shoreline and inland may have resulted in disparities in activities and abundances of prey, thereby influencing foraging behavior. Birds also may have altered foraging behavior in response to shoreline/inland differences in the kinds of arthropods that were available within a habitat.

The most obvious spatial disparity in prey for migrants was the abundance of adult midges in shoreline habitats. These insects were strongly associated with the lakeshore; beyond 0.40 km from shoreline, midge abundance dropped to near zero (DNE unpubl. data). Midges commonly rest on nearshore vegetation in high densities, and both field obser-

ations and our results suggest that birds foraged heavily on these insects. In temperate habitats, mating swarms of midges are temperature dependent (R. J. Smith and F. R. Moore unpubl. data); depending on the species, they begin to swarm at a critical minimum temperature of about 10° C (Armitage 1995).

Redstart foraging preferences corresponded with the activity and presence/absence of midges. For instance, redstart foraging activity was most intense during early morning when temperatures often were below 10° C. Lower shoreline temperatures may have delayed swarming until later in the day, resulting in high densities of substrate-bound (resting) midges. Thus, resting midges may have elicited, at least in part, the more-frequent gleaning observed in shoreline areas than inland areas. Furthermore, the differential use of northern white cedar suggests that midges may be an important food resource; redstarts used cedar significantly more at the shoreline compared to inland, even though there was no significant shoreline/inland difference in cedar density across the study area (DNE unpubl. data). Moreover, shoreline redstarts did not depart from random use of cedar while inland birds foraged in cedar less than expected. This differential use of cedar may reflect differential midge abundance. Birds shifted foraging away from cedar inland, where few midges occurred. This reduction in use of inland cedar suggests that suitable prey items, other than midges, were not abundant in cedar.

Similar results were documented in Black-throated Green Warblers foraging in cedar in the same area (Smith et al. 1998). Birds used cedar as expected at the shoreline during spring migration and less than expected inland. During the breeding season and fall migration, when midges were not abundant in shoreline habitats (DNE unpubl. data), Black-throated Green Warblers used cedar significantly less. The shoreline/inland differences in cedar use by both redstarts and Black-throated Green Warblers, and the decline in shoreline use by Black-throated Green Warblers during the breeding season and fall migration, suggest that birds foraged in cedar in response to the presence of midges and that prey items other than midges were not abundant in cedar.

Constructive replication in the behavioral

sciences is rare (Martin and Bateson 1993). We have identified concordant results between two warbler species that are rather disparate foragers. Black-throated Green Warblers include a high percentage of gleans as part of their foraging repertoire (Morse 1993), whereas American Redstarts use relatively fewer gleans and more aerial-directed foraging maneuvers (Sherry and Holmes 1997). Similarities in foraging between these two species reduce the likelihood that our results are spurious, and they provide additional support for the hypothesis that aquatic insects are a critical early season resource for landbirds during spring migration in Michigan's eastern Upper Peninsula.

Intercontinental landbird migrants often outpace the phenological development of vegetation and terrestrial invertebrates as they move north during spring migration (Slagsvold 1976, Ewert and Hamas 1995), arriving on their breeding grounds well before vegetation is fully leafed out and food becomes abundant (Slagsvold 1976, Nolan 1978, Perrins 1996, Nystrom 1997). Arrival of migrants breeding in northern Michigan may precede completion of leaf development by up to 4 weeks (RJS unpubl. data). Early arrival also increases exposure to inclement weather, including late season snowstorms, low temperatures, or extended periods of rain (Whitmore et al. 1977, Zumeta and Holmes 1978, Ewert and Hamas 1995, Aebischer et al. 1996, Merkle and Barclay 1996). Midges may provide the energy necessary for survival during severe weather or, under better conditions, energy for fat deposition, allowing a timely return and beginning of breeding (Alerstam and Lindström 1990, Rowe et al. 1994, Smith and Moore 2003). The quality of nearshore areas in Michigan's eastern Upper Peninsula appears to be augmented by the presence of adult aquatic insects, which provide a critical food source prior to the appearance of leaves and emergence of phytophagous insects.

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USE OF OAK HAMMOCKS BY NEOTROPICAL MIGRANT SONGBIRDS: THE ROLE OF AREA AND HABITAT

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ABSTRACT.—Many species of Neotropical migrant songbirds have declined in recent decades, due in part to loss and fragmentation of stopover habitat. To properly manage forested landscapes for migrating songbirds, information is needed on how size and habitat structure of forest patches influence their use by migrants during stopover. We conducted surveys of Neotropical migrant birds in eight oak hammocks of varying size (0.32–3.08 ha) at the Savannah National Wildlife Refuge, Jasper County, South Carolina during spring migration 1999 and 2000 and fall migration 1999. Hammock size was the most important factor related to number of total species, species per day, individuals per day, and density of migrants. Differences in vegetation structure and patchiness among hammocks did not explain differences in migrant abundance. Density of migrants tended to be higher in smaller hammocks, particularly during spring. Hammock use was generally similar between seasons and years. Two forest-interior breeding species occurred more often in the largest hammocks, suggesting that interior species are susceptible to forest fragmentation while en route. We suggest that protection of larger (versus smaller) tracts of forest is more beneficial to migrating songbirds, especially declining forest interior species. *Received 22 April 2003, accepted 19 April 2004.*

In recent decades many species of Neotropical migrant birds have undergone population declines (Faaborg and Arendt 1992, Gauthreaux 1992, Peterjohn et al. 1995). Although these declines may be linked to loss of habitat on the breeding grounds in North America and wintering grounds in Mexico, the Caribbean, and Central and South America (Robbins et al. 1989b, Askins et al. 1990), the loss of suitable stopover habitat has also been implicated (Moore et al. 1990). Thus, an important first step in managing land appropriately for en route migrant landbirds is to identify habitat features that are important in selection of stopover sites.

The maritime forests along the southeast Atlantic and Gulf coasts are a valuable resource for songbirds (Cohrs and Cohrs 1994, Moore et al. 1995). On the coasts of South Carolina, Georgia, and northernmost Florida, maritime forests are dominated by live oaks (*Quercus virginiana*), and occur as large contiguous patches of forest on barrier islands, the immediate mainland, and as small patches (oak hammocks) scattered among coastal marshes. Although contiguous patches of maritime forest occur on barrier islands and the

adjacent mainland, oak hammocks are natural formations located on small (<0.4–500 ha) patches of well-drained soil among coastal marshes isolated from other oak hammocks and forests. In six coastal Georgia counties, more than 1,200 oak hammocks have been identified, with 85% of these smaller than 4 ha (Georgia Department of Natural Resources 2002). The rising value of coastal property has led to development of large patches of maritime forest (large oak hammocks and barrier islands) as well as smaller and more isolated hammocks (U.S. Fish and Wildlife Service 1993, Georgia Department of Natural Resources 2002).

As development reduces the amount of maritime forest cover, migrant birds may experience reduced refueling rates and may incur increased en route mortality (Petit 2000). Stopover ecology of Neotropical migrant songbirds along the southeastern coast has received little attention despite recent songbird declines and rapid coastal development. In addition, no studies have been conducted on songbird use of hammocks during migration. Hammocks are accessible only by boat and the expense and difficulty in accessing hammocks has prevented thorough songbird studies from being conducted. Oak hammocks may be critical habitat for Neotropical migrant songbirds (Cox 1988), but little is known about how migrants use hammocks during stopover (Hillestad et al. 1975, Cox 1988,

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Cohrs and Cohrs 1994). Lack of knowledge on hammock use by migrants may hamper appropriate management of this habitat along the coast of the southeastern United States.

A representative example of oak hammocks along the southeastern coast occurs at Savannah National Wildlife Refuge (SNWR), Jasper County, South Carolina. Several hammocks are readily accessible via a series of impoundments used to control water levels. Hammock size distribution and vegetative communities are similar to those found elsewhere in Georgia and along the southeastern Atlantic coast (Georgia Department of Natural Resources 2002), making SNWR an ideal location to study songbird migration.

We assessed migrant stopover use of oak hammocks to determine whether (1) abundance of migrating Neotropical songbirds increases with hammock size, (2) vegetation structure influences the abundance and diversity of migrants, and (3) edge and forest interior species use hammocks differently.

METHODS

Study area.—We conducted our study from April 1999 through May 2000 at the SNWR (32° 15' N, 81° 11' W), Jasper County, South Carolina. The study site is located on the lower coastal plain approximately 16 km from the Atlantic Ocean and comprises 4,306 ha of freshwater marsh and scattered forest. We located 11 oak hammocks on SNWR that were accessible from a series of impoundments used to control water levels. We selected eight of these hammocks for surveys so as to span the range in size of fragments (0.32, 0.57, 1.05, 1.13, 1.29, 1.70, 1.86, and 3.08 ha) at SNWR; this range represents most hammocks in the coastal region. Study hammocks were isolated from one another by >0.4 km of freshwater marsh and were located 1.6–3.0 km from adjacent forests. Hammock isolation reduced movement of migrants among hammocks and adjacent forests during surveys. The three hammocks not selected were difficult to access or near adjacent forest. We measured the area of each fragment ($\pm 5\%$) with a Corvallis Microtechnology MC-V Global Positioning System differentially corrected to the Charleston, South Carolina base station.

Bird surveys.—During spring 1999 and 2000 (10 April–12 May), we surveyed birds

in each hammock 26–29 times, and, during fall 1999 migration (25 September–30 October), we surveyed each of five hammocks 23 times. Surveys were conducted 4–5 times weekly. We surveyed fewer hammocks in fall to allow for an increased number of surveys per hammock in one field season. We chose the two largest and two smallest hammocks for surveys during fall migration and randomly chose a fifth (1.29 ha) from the remaining four hammocks.

We estimated songbird abundance and diversity using a modified line transect. Because some study plots were small (<0.6 ha), we could not use standard point or line transect techniques and therefore did not collect distance data. We conducted our surveys along a pre-selected circular path through the generally round forest patches. We followed a path that allowed for an audible and/or visual survey of the entire hammock and recorded the presence of all birds observed within the hammock. Survey duration varied among hammocks, however we surveyed each hammock with constant effort per unit area (~ 2.1 ha/hr). We followed the same route during each survey. Vegetation height, structure, and density were similar among hammocks, thus our ability to detect birds within and among hammocks was similar. We surveyed hammocks in random order during the first 3.5 hr after local sunrise. We did not conduct surveys during rain or when winds were >24 km/hr. We defined Neotropical migrants according to Hunter et al. (1993).

The migrants recorded in this study likely spent most of the day in the hammock where they were observed; thus, surveys were independent on each day. We based this on the following: (1) we recorded only one instance of migrants moving between hammocks during surveys; (2) migrants often complete nocturnal flight before civil twilight (Graber 1968, Able 1970, Bellrose 1971), so most of the movement between hammocks probably occurred before we began the first survey after sunrise each morning; and (3) migrants typically move only short distances during stopover (Aborn and Moore 1997; J. Farrington pers. comm.; J. Buler pers. comm.).

We attempted to avoid recounting individuals within a hammock during each survey. In spring, a small number of migrants discontin-

ued migration and became summer residents during our survey period. If we repeatedly observed an individual of any locally breeding Neotropical species in the same location exhibiting nesting behavior (e.g., courtship, nest building), we considered the bird a local breeder and removed the individual from migration surveys. We conducted surveys to quantify the breeding bird community in each hammock during late May and early June, confirmed local breeding pairs, and removed those birds (<20 birds) from our migration surveys. We removed no birds from fall surveys because we conducted all surveys after the breeding season, and few individuals were winter residents (SGS pers. obs.). We suspect some birds held territories during both spring and fall migration and the same individual may have been recorded on multiple surveys. The lack of temporal independence is inherent in all migration studies involving surveys of unbanded birds, however, from our observations we suspect daily turnover rates were large (>90%) in all hammocks, with few individuals staying for multiple days. All surveys were conducted by the same individual (SGS).

Habitat characteristics.—We quantified habitat within each hammock in spring 1999 following James and Shugart (1970). We used 0.04 ha plots to quantify $\geq 25\%$ of the area of each hammock. We measured (1) basal area of trees ≥ 10 cm diameter at breast height (dbh), (2) percent canopy cover, (3) percent herbaceous ground cover, (4) litter depth, (5) number of trees ≥ 10 cm dbh, (6) number of yaupon (*Ilex vomitoria*) stems <10 cm dbh, and (7) number of other stems <10 cm dbh. We estimated yaupon stem density separately because yaupon is the dominant understory plant and it may provide fruit resources for fall migrants (Grimm 1983).

The canopies of the oak hammocks were dominated by mature oaks (*Q. virginiana*, *Q. laurifolia*, and *Q. nigra*), sweetgum (*Liquidambar styraciflua*), sugarberry (*Celtis laevigata*), chinaberry (*Melia azedarach*), and Chinese tallow (*Sapium sebiferum*). Pines (*Pinus elliotii*, *P. palustris*) and bald cypress (*Taxodium distichum*) were present, but were a minor part of the canopy. Understory vegetation was comprised primarily of yaupon, cherry laurel (*Prunus caroliniana*), red maple (*Acer*

rubrum), saw palmetto (*Serenoa repens*), greenbrier (*Smilax* spp.), mulberry (*Morus* spp.), wax myrtle (*Myrica cerifera*), and beautyberry (*Callicarpa americana*).

Statistical analyses.—We checked data for normality and homogeneous variances before conducting parametric tests. We used paired *t*-tests (data paired by hammocks) to examine differences in number of species per day, individuals per day, and density of migrants between years and seasons. We used linear regression to assess whether migrants consistently preferred certain hammocks across years or seasons. We used ANOVA to test for added variance among hammocks in number of individuals and species per day (abundance) and density (number of individuals per ha). The added variance addresses random effects varying among groups (individual hammocks) and partitions variation into two types: (1) day-to-day variation within hammocks, and (2) variation among hammocks.

We used principal components analysis (PC) of the correlation matrix of the original habitat variables to reduce vegetation data into fewer variables. For those PC axes with eigenvalues >1, we calculated mean PC scores and the variance in PC scores for each hammock and then used ANOVA to test for vegetation differences based on PC scores.

To assess the effects of area (log transformed) and vegetation structure on the number of species per day, individuals per day, and density we used least-squares linear regression. Slope (*b*) represents the direction of the relationship between hammock size or vegetation and the associated variable (abundance or density). A positive slope indicates a direct relationship, while a negative slope indicates an inverse relationship between the treatment (hammock size or PC score) and the variable (abundance or density). Analysis of how individual species used hammocks of varying size and vegetation structure included only species recorded on $\geq 7\%$ of all counts during the season being analyzed. We set $\alpha = 0.05$ and conducted all statistical analyses using JMP 3.02 Statistical Software (SAS Institute, Inc. 1995).

RESULTS

We recorded 41 Neotropical species with a mean of 27.4 ± 2.8 (SE) individuals per day

TABLE 1. Richness, abundance, and density of Neotropical migrants in oak hammocks at the Savannah National Wildlife Refuge, Jasper County, South Carolina, 1999–2000.

	Hammock area (ha)							
	0.32	0.57	1.05	1.13	1.29	1.70	1.86	3.08
Spring 1999								
Total species per season	15	12	16	22	14	19	27	25
Mean number of species per day	2.3	2.7	3.2	3.9	2.1	4.3	6.5	5.7
Mean number of individuals per day	3.1	4.4	5.2	6.7	4.1	7.3	11.3	8.3
Mean density (number per ha)	9.6	7.7	5.0	5.9	3.2	4.3	6.1	2.7
Fall 1999								
Total species per season	12	12			18		21	21
Mean number of species per day	3.0	2.9			4.0		5.4	8.3
Mean number of individuals per day	7.2	5.9			9.2		12.6	32.9
Mean density (number per ha)	22.5	10.4			7.1		6.8	10.6
Spring 2000								
Total species per season	12	16	18	20	16	19	21	21
Mean number of species per day	2.2	2.7	3.2	3.0	3.2	3.0	3.9	6.3
Mean number of individuals per day	4.0	4.5	4.7	3.8	4.4	3.9	5.3	10.1
Mean density (number per ha)	12.5	7.9	4.5	3.4	3.4	2.3	2.8	3.3

(sum for all hammocks) during spring migration. We recorded 30 species with a mean of 67.3 ± 7.9 (SE) individuals per day (sum for all hammocks) during fall. See Somershoe (2000) for a complete species list.

During spring, the abundance and density of migrants per day did not differ among years. Density of migrants ($F_{1,7} = 12.92$, $P = 0.011$, $R^2 = 0.68$) in each hammock in 2000 could be predicted from 1999. On the other hand, number of species per day ($F_{1,7} = 5.08$, $P = 0.064$, $R^2 = 0.46$) and individuals per day ($F_{1,7} = 1.21$, $P = 0.32$, $R^2 = 0.17$) were less predictable from year to year. Hammocks sampled in spring and fall ($n = 5$) were used similarly in terms of number of species per day ($F_{1,4} = 15.07$, $P = 0.030$, $R^2 = 0.83$) and density ($F_{1,4} = 12.14$, $P = 0.040$, $R^2 = 0.80$), but the number of individuals per day ($F_{1,4} = 15.12$, $P = 0.067$, $R^2 = 0.73$) was less predictable between seasons.

Richness, abundance, and density of Neotropical migrants varied among hammocks (Table 1). During spring, 81–90% of the variation in species per day, number of individuals per day, and density of Neotropical migrants was attributable to consistent day-to-day differences within hammocks. During fall, 46–71% of the variation in abundance and density was explained by differences within hammocks.

We detected a significant relationship between hammock area and number of total species, species per day, individuals per day, and density of migrants in both spring 1999 and 2000, except for number of individuals per day in spring 2000 (Table 2). Total species per season and species per day were the only variables that varied by area during fall 1999. Larger hammocks attracted more species and more individuals (positive slope); smaller hammocks tended to hold a higher density of migrants (negative slope; Table 2).

Three principal components accounted for 63.8% of the total variation in vegetation. PC1 described a gradient from relatively open forest with large amounts of herbaceous ground cover to denser forest with deep litter and smaller amounts of herbaceous ground cover (27.8% of the variation). The gradient described by PC2 ranged from large amounts of total basal area and yaupon stems to areas with large numbers of trees and other stems (21.5% of the variation). PC3 depicted a trend from large numbers of other stems and a complete canopy to areas with a large mean litter depth (14.5% of the variation). Vegetation structure differed significantly among hammocks only along the first principal component axis ($F_{7,56} = 5.77$, $P = 0.001$), while no significant differences were found along PC2 ($F_{7,56} = 1.74$, $P = 0.13$) and PC3 ($F_{7,56} =$

TABLE 2. Linear regressions of hammock area on the number of species per season, species per day, individuals per day, and density of Neotropical migrants among hammocks at the Savannah National Wildlife Refuge, Jasper County, South Carolina, 1999–2000. R^2 values represent amount of variation in species per season, mean species per day, individuals per day, and density explained by among-hammock variation in area; b values represent the slope of the relationship between hammock area and the associated variable.

	Spring 1999			Fall 1999			Spring 2000		
	P	R^2	b	P	R^2	b	P	R^2	b
Total species per season	0.044	0.52	12.8	0.011	0.91	11.0	0.002	0.82	12.2
Number of species per day	0.034	0.55	3.9	0.046	0.78	5.0	0.015	0.65	3.3
Number of individuals per day	0.029	0.57	6.6	0.12	0.61	21.9	0.10	0.38	4.2
Density (number per ha)	0.020	0.62	-6.1	0.17	0.52	-11.7	0.002	0.81	-10.4

1.96, $P = 0.082$). The structure (mean PC score) and patchiness (variance in PC scores) of the vegetation in hammocks was unrelated to variation in richness, abundance, and density of migrants in both spring and fall (all $P \geq 0.18$; Table 3).

We recorded 12 species during spring and 11 species during fall on at least 7% of all counts (Table 4). Although eight species showed significant relationships between numbers of individuals per day and hammock area in spring, little variation in the relationship was accounted for by hammock area (all $R^2 \leq 0.07$). Of 10 species detected significantly more often in large hammocks during the fall, Eastern Wood-Pewee (*Contopus virens*; $P < 0.001$, $R^2 = 0.27$), Blue-gray Gnatcatcher (*Poliopitila caerulea*; $P < 0.001$, $R^2 = 0.22$), American Redstart (*Setophaga ruticilla*;

$P < 0.001$, $R^2 = 0.27$), and Northern Waterthrush (*Seiurus noveboracensis*; $P < 0.001$, $R^2 = 0.39$) had substantive amounts of variation explained by the regression. We also found an interesting distribution of several species across hammocks. During spring, we did not detect Northern Waterthrushes in the smallest hammock, detected them only once in the next smallest hammock (0.57 ha), but we detected them regularly in the larger hammocks. During fall, we found four species in only the three largest hammocks: Eastern Wood-Pewee, Northern Parula (*Parula americana*), Palm Warbler (*Dendroica palmarum*), and Northern Waterthrush. We detected Eastern Wood-Pewee and Northern Waterthrush in the largest hammock on 71 and 96% of all counts, respectively, and did not record them on any counts in the two smallest hammocks. A sig-

TABLE 3. Linear regressions of PC1 score (vegetation structure) and variance in PC1 score (vegetation patchiness) on the number of species per season, species per day, individuals per day, and density of Neotropical migrants among hammocks at the Savannah National Wildlife Refuge, Jasper County, South Carolina, 1999–2000. Abundance, richness, and density were not related to vegetation structure (all $P \geq 0.18$). R^2 values represent amount of variation in number of species per season, species per day, individuals per day, and density explained by among-hammock variation in vegetation; b values represent the slope of the relationship between vegetation structure or vegetation patchiness and the associated variable.

	Spring 1999			Fall 1999			Spring 2000		
	P	R^2	b	P	R^2	b	P	R^2	b
Vegetation structure									
Total species per season	0.67	0.03	-0.90	0.64	0.08	0.99	0.84	0.01	-0.32
Number of species per day	0.55	0.06	-0.37	0.83	0.02	-0.22	0.99	0.00	-0.01
Number of individuals per day	0.81	0.01	-0.25	0.70	0.06	-1.99	0.75	0.01	-0.26
Density (number per ha)	0.18	0.28	-1.15	0.22	0.44	-3.18	0.49	0.08	-0.07
Vegetation patchiness									
Total species per season	0.31	0.17	-1.15	0.99	0.00	0.02	0.30	0.17	-0.89
Number of species per day	0.19	0.26	-0.42	0.63	0.09	-0.29	0.74	0.02	-0.09
Number of individuals per day	0.28	0.19	-0.60	0.59	0.10	-1.54	0.71	0.02	-0.17
Density (number per ha)	0.54	0.07	-0.31	0.84	0.02	-0.34	0.89	0.00	0.13

TABLE 4. Linear regressions of hammock area (ha) and vegetation structure (mean PC1 score) on the number of Neotropical migrant individuals per day among hammocks at the Savannah National Wildlife Refuge, Jasper County, South Carolina, 1999–2000. We detected substantial variation ($R^2 > 0.22$) between hammock area and daily abundance for four species during fall 1999 migration (boldface). Neither hammock area nor vegetation structure explained much of the variation in daily abundance for other species in either season (all $R^2 \leq 0.18$). Species lacking information for either spring or fall indicate that minimum occurrence criteria were not satisfied (see text).

Species	Combined spring 1999 and 2000					Fall 1999				
	% counts ^a	Area		Vegetation structure		% counts ^a	Area		Vegetation structure	
		P	R ²	P	R ²		P	R ²	P	R ²
<i>Contopus virens</i> ^b						25	<0.001	0.27	0.70	0.00
<i>Myiarchus crinitus</i> ^b	30	0.099	0.03	0.99	0.00					
<i>Tyrannus tyrannus</i> ^b	33	0.044	0.02	<0.001	0.05					
<i>Vireo griseus</i> ^b						30	0.001	0.12	0.82	0.00
<i>Poliophtila caerulea</i> ^b	28	<0.001	0.07	0.01	0.05	39	<0.001	0.22	0.57	0.00
<i>Dumetella carolinensis</i> ^b	32	0.25	0.00	0.29	0.01	74	0.003	0.08	0.62	0.00
<i>Parula americana</i> ^b	21	<0.001	0.06	0.13	0.01	17	0.001	0.09	0.005	0.07
<i>Dendroica caerulescens</i> ^c	16	0.005	0.03	0.57	0.00	14	0.68	0.00	0.11	0.02
<i>Dendroica palmarum</i> ^b						9	0.004	0.07	0.54	0.00
<i>Dendroica striata</i> ^c	9	0.005	0.03	0.61	0.00					
<i>Mniotilta varia</i> ^c	15	0.003	0.04	0.83	0.00					
<i>Setophaga ruticilla</i> ^c	22	0.10	0.01	0.94	0.00	61	<0.001	0.27	0.07	0.03
<i>Seiurus noveboracensis</i> ^b	7	<0.001	0.07	0.31	0.00	33	<0.001	0.39	0.13	0.02
<i>Geothlypis trichas</i> ^b	50	0.007	0.03	0.08	0.01	57	<0.001	0.18	0.032	0.04
<i>Passerina cyanea</i> ^d						57	<0.001	0.12	0.13	0.02
<i>Icterus spurius</i> ^d	23	0.92	0.00	0.13	0.01					

^a Percent occurrence over all counts.

^b Interior species.

^c Interior/edge species.

^d Edge/scrub species (definitions follow Whitecomb et al. 1981, Robbins et al. 1989a, Holmes 1994, Wilson 1996).

nificant relationship between individuals per day and vegetation structure was detected for a few species, but only a small amount of the variation was explained by vegetation (all $R^2 \leq 0.07$; Table 4).

DISCUSSION

Larger oak hammocks along the South Carolina coast attract larger numbers of species, species per day, and individuals per day, while smaller hammocks tend to have higher densities of migrants. A substantial portion of variation in migrant abundance and density in spring was due to day-to-day differences within hammocks, while among hammock variation explained migrant distribution in fall. This implies that there are features of oak hammocks that are predictably associated with use by Neotropical migrants.

One of the features is clearly size: larger hammocks contained more species and more individuals. Others also have found a positive species-area relationship for migrant birds in

forest patches (Martin 1980, Cox 1988). The simplest explanation for this pattern is that migrants sort into hammocks at random as they arrive over the study area. If so, density of migrants should be similar among hammocks of different size. Our results show that large hammocks attract more individuals but small hammocks support higher densities of migrants (Tables 1, 2), which is inconsistent with random sorting (Martin 1980). Because many migrants discontinue nocturnal flight before sunrise, they may randomly choose a hammock upon landing and select more suitable habitat or hammocks before sunrise. As a result, we might expect the distribution of migrants after hammock selection to be nonrandom, as we found.

Although Martin (1980) suggested that habitat diversity may be a better predictor of abundance of migrants than area, we did not detect a relationship between vegetation structure and migrant richness, abundance, or density. Although migrants exhibit habitat pref-

erences (Bairlein 1983, Lindström 1989), at the scale of our analysis, among-hammock sorting of the migrant assemblage was not correlated to features of the vegetation.

If songbirds select migratory habitat in a way that is similar to how they select breeding habitat (Petit 2000), forest interior specialists also may show preferences for larger forest patches along the migration route (Whitcomb et al. 1981). Six species (Eastern Wood-Pewee, Blue-gray Gnatcatcher, Northern Parula, Palm Warbler, American Redstart, and Northern Waterthrush) were found most often in large hammocks; thus, small hammocks (<0.5 ha) may not provide adequate habitat. This suggests that fragmentation of forested stop-over sites may be detrimental to these species. Species such as the Eastern Wood-Pewee, which is declining in the eastern portion of its range (Breeding Bird Survey; Peterjohn et al. 1995), might suffer from the effects of fragmentation en route as well as on the breeding and wintering grounds.

Number of individuals per day, likely the most variable of measurements, differed between seasons and years because of the large variation in the daily number of individuals inherent in studies of migration. Although sources of variation in migrant abundance and density among hammocks differed between seasons, general patterns of similar numbers of species per day and density between years and seasons suggest that migrants are using similar criteria in selecting hammocks. The hammocks at SNWR are similar to others found in South Carolina and along the southeastern Atlantic coast. Thus, consistent patterns in bird abundance and density between years and seasons may be applicable to other hammocks and our data may provide reliable information for developing management guidelines.

Although oak hammocks are not remnants of larger, contiguous forest, migrants likely use the same criteria in selecting hammocks and fragments of maritime forest. Development on barrier islands will fragment contiguous maritime forest, resulting in small patches of forest surrounded by unsuitable habitat (i.e., houses, roads, etc.). Many of these new fragments will be of comparable size to natural oak hammocks and the observed patterns of migrant richness, abundance, and density in

hammocks at SNWR may apply to these new fragments.

Our results suggest that management should emphasize preserving all hammocks for migrating songbirds; however, larger hammocks may be more beneficial to forest interior species. Future research should address the issues of habitat use, resource availability, and stop-over success in hammocks and remnant forest fragments.

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ACTIVITY BUDGETS OF SUMMER TANAGERS DURING SPRING MIGRATORY STOPOVER

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ABSTRACT.—We radio-tracked Summer Tanagers (*Piranga rubra*) at a Gulf coast stopover site to study en route activity budgets. Tanagers were inactive a majority of the time, with scanning, foraging, and preening being the next most commonly observed activities. When foraging, tanagers primarily used sallying to capture a variety of insect prey. Possible explanations for inactivity during stopover include the need for rest following prolonged flight, muscle repair, reduced digestive capacity, and the short distance remaining to the breeding grounds. Received 29 June 2003, accepted 23 March 2004.

Knowledge of stopover biology is critical to our understanding of the population dynamics of migratory birds (Moore et al. 1995). One area of stopover biology where we know little is activity budgets of migrants en route. Simply put, what does a migrant do from the time it arrives at a stopover site until it resumes migration? Activity budgets can reveal how well migrants meet energetic demands in relation to food resources (King 1974), and also may reflect habitat suitability: migrants may devote more time to foraging in habitats where food resources are low. Activity budgets can also reveal behavioral plasticity that may occur during migration, which tells us how adaptable migrants may be during passage (Greenberg 1990, Martin and Karr 1990). How much time a migrant spends foraging, being vigilant, flying, and engaged in other behaviors is therefore important in helping us to understand differences in habitat selection, mass change, vulnerability to predation, and stopover length among individual migrants.

Part of the reason for the lack of information on activity budgets en route stems from the difficulties of observing songbirds for extended periods of time. One way of overcoming this problem is to use radiotelemetry (Williams 1990). We attached transmitters to Summer Tanagers (*Piranga rubra*) to monitor their activity during stopover following spring trans-Gulf migration. We predicted that Sum-

mer Tanagers would spend most of their time foraging, since they likely would need to replenish fat stores following trans-Gulf flight (Moore and Kerlinger 1987). We expected that scanning and preening would be the next most common activities, since avoiding predation and feather maintenance are also important aspects of stopover.

METHODS

Research was conducted off the coast of Mississippi, on Horn Island (30° 14' N, 88° 40' W). The island is approximately 22 km long and 1 km wide. We recognized four relatively discrete habitat types: pine forest, scrub/shrub, marsh/meadow, and relic dune (see Moore et al. 1990 for descriptions).

We captured 24 Summer Tanagers in mist nets (12 × 2.6 m, 30-mm mesh) and fitted each with a transmitter. Transmitters (Custom Telemetry and Consulting, Watkinsville, Georgia) weighed 1.3–1.4 g, had a range of 1 km, and a lifespan of 7 days. A transmitter was not attached if the weight of the transmitter exceeded 5% of the bird's body weight (Cochran 1980, Aldridge and Brigham 1988). The weight of radioed tanagers ranged from 25.4 to 32.8 g. We attached transmitters to the base of the central tail feathers using cyanoacrylate glue and a small cable tie, and released birds at their place of capture. We tracked tanagers continuously until either migration resumed or the transmitter failed. Here, we analyze only data for the first day of tracking a given bird; tracking time varied from 4 to 11 hr/bird. Each bird, rather than each movement, was treated as a sample unit to avoid the problem of pseudoreplication (Aebischer et al. 1993), since the movements might not be independent of one another.

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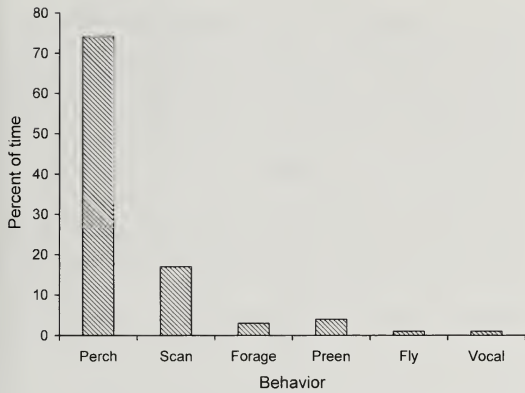


FIG. 1. Activity budgets for all Summer Tanagers on Horn Island, Mississippi while in sight during spring migrations of 1992–1994.

We observed activities of tanagers using 10 × 50 binoculars, and dictated observations into a tape recorder for later transcription. Behavioral activities recorded were perching (bird totally inactive), flying (any non-foraging or non-evasive flight), foraging (consuming food), scanning (perched and actively looking around), preening (feather maintenance), aggression (displacing or attacking a conspecific or heterospecific), escape (fleeing or evading a conspecific or heterospecific, including a predator), and vocalizing (singing or calling). Foraging methods (Remsen and Robinson 1990) included gleaning (picking food items from a nearby substrate, excluding the ground, without full extension of the body), sallying (flying from a perch to attack a food item in the air and then returning to the perch), frugivory (consuming fruit), and ground foraging (flying down to or moving along the ground and picking food items). When a tanager was not in view, we categorized the bird as being either perched, active, or flying. For birds classified as “perched,” there was no variation in signal strength or direction. For tanagers that were “active,” the signal direction fluctuated, but still stayed within a confined area. Based on signal strength, we could tell when birds were within about 50 m, so we knew the bird’s movements were localized. Signals of birds that were flying continuously faded in one particular direction, indicating the birds were steadily moving away from the receiver.

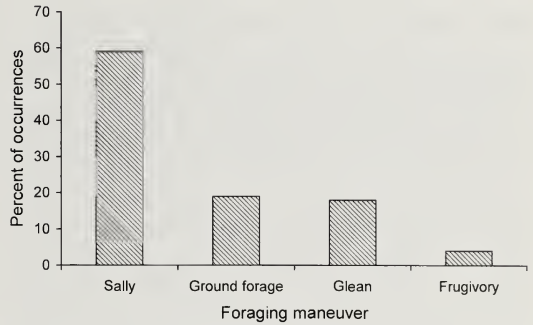


FIG. 2. Foraging methods used by Summer Tanagers on Horn Island, Mississippi during spring migrations of 1992–1994.

To examine the possibility that transmitters might influence tanager behavior, we observed tanagers without transmitters on days when we were not radio-tracking. We recorded the same behaviors as for birds carrying transmitters. We used a chi-square contingency test with a significance level of 0.05 to compare the proportion of time that radio-marked and non-radio-marked tanagers spent in different activities (Zar 1984).

RESULTS

We radio-tracked 24 Summer Tanagers during spring migrations of 1992–1994, for a total of 190 hr. Of total tracking time, 88 hr (45%) were direct visual observations. Visual observations revealed that the birds spent 74% (range: 22–97%) of their time perched (Fig. 1). Scanning, preening, and foraging were, respectively, the next most common activities. Foraging techniques included sallying (59%; range: 0–96%), gleaning and ground foraging combined (37%; range: 0–99%), and frugivory (4%; range: 0–92%) (Fig. 2). Frugivory was low despite an abundance of yaupon (*Ilex vomitoria*) and greenbrier (*Smilax* spp.) berries on the island (J. Clark unpubl. data). Of the prey items we could identify ($n = 25$), all but one were insects: Lepidoptera ($n = 8$), Odonata ($n = 5$), Coleoptera ($n = 4$), Hymenoptera ($n = 4$), Orthoptera ($n = 2$), and Diptera ($n = 1$). One tanager attempted to eat a green anole (*Anolis carolinensis*; Aborn and Froehlich 1995). The only other activity observed was sleeping. Three birds were observed during daylight hours with their feathers fluffed, eyes closed, and bills tucked into

their backs for 20–40 min each. When not in view, tanagers spent approximately equal amounts of time perched (50%) and active (49%), spending only 1% of the time in flight.

We observed 17 non-radio-marked Summer Tanagers for a total of 54 min. These birds spent 63% of their time perched, 23% scanning, 10% foraging, and 3% flying. Compared with visual observations of all radio-tracked tanagers, there was no significant difference in the proportion of time devoted to the different activities ($\chi^2 = 6.5$, $P = 0.090$). We concluded that transmitters did not influence the behavior of the radioed tanagers.

DISCUSSION

Overall, tanagers spent most of their time perched, with relatively little time spent scanning and foraging. The low percentage of time we observed tanagers foraging contradicts our prediction that the birds would spend much of their time foraging. While information on activity during migration is limited, the foraging time of wood-warblers (Parulidae) during spring migration is reported to be 43–68% (Graber and Graber 1983). During winter, Summer Tanagers are known to perch inactively and then make sudden movements to forage (Isler and Isler 1999). Scarlet Tanagers (*Piranga olivacea*) often exhibit relatively long periods of inactivity while searching for insects during the breeding season (Robinson and Holmes 1982). Thus, low levels of activity may be typical for temperate-breeding tanagers, even during migration.

Inactivity during migratory stopover might reflect the need for rest following trans-Gulf flight. Our observations of tanagers sleeping support this notion. Trans-Gulf migrants must make an 18–24 hr non-stop flight (Moore et al. 1990), which entails loss of an entire night's sleep. Captive Yellow-rumped Warblers (*Dendroica coronata*) induced into spring migratory condition and deprived of one night's sleep showed reduced food handling ability and vigilance compared with warblers that were allowed to sleep (High 1996). Palearctic migrants have also been shown to sleep following trans-Mediterranean flight, which is comparable in flight time and distance to trans-Gulf migration (Schwilch et al. 2002). Schwilch et al. (2002) go on to suggest that sleep is second in importance only

to replenishing water and glycogen for migrants that have made long flights. Therefore, spending time resting may increase the likelihood that a migrant will be able to forage efficiently, avoid predation, and successfully complete its migration.

Second, stopover inactivity may be a way of coping with muscle damage. Flight muscle analyses of Horned Larks (*Eremophila alpestris*) that experienced overnight fasting revealed significant depletion of muscle protein and other muscle components (Swain 1992). In particular, sarcoplasm, which is important for muscle contraction, and glycolytic capacity, which is important for intense, short-duration flights were both significantly reduced (Swain 1992). If trans-Gulf migrants experience similar effects, then they may need to allow their bodies to recover from the prolonged exertion. The loss of glycolytic capacity in particular might impair the tanagers' ability to perform foraging maneuvers like sallying.

Third, inactivity may be an effect of reduced digestive function. Experiments with Garden Warblers (*Sylvia borin*) subjected to several nights of fasting revealed that the birds had a reduced metabolic rate, which was attributed to a reduction of digestive function (Klaassen and Biebach 1994). This reduction in digestive function and metabolic rate, in turn, led to reduced activity levels. Taken together, these changes lead to a reduction in energy expenditure that allows migrants to fly greater distances on a given amount of fuel. Trans-Gulf migrants may also experience such reductions, and the lack of activity seen in the tanagers may have been a reflection of this phenomenon.

A fourth explanation for the lack of activity in Summer Tanagers may relate to the remaining distance to the breeding grounds. Many Summer Tanagers breed in Mississippi and Alabama (Robinson 1996), so the birds we observed may have been near the end of their migration and therefore may not have needed to deposit large amounts of fat. Translated into migratory flight distance, tanagers carrying surplus fat have could have flown an average of 513 km (able to reach the Mississippi-Tennessee border), whereas tanagers lacking fat stores could have flown only 162 km (enabling them to reach southern Missis-

ssippi) (Pennycuick 1992). Thus, many of the Summer Tanagers stopping on Horn Island may not need to spend much time foraging, and can devote more time to other needs, such as rest or avoiding predation.

On both the breeding and wintering grounds, Summer Tanagers generally use salyng and gleaning to capture insects, primarily Hymenoptera, Orthoptera, and Coleoptera (Robinson 1996, Isler and Isler 1999), largely in agreement with our data. The small amount of frugivory we observed may be typical, as Robinson (1996:6) reports that Summer Tanagers "may take some [fruit] during breeding and migration." Ground foraging is used by Scarlet Tanagers on occasion (Prescott 1965), but has not been recorded previously for Summer Tanagers (Robinson 1996).

Habitats that provide shelter and concealment may be just as important to migrants as habitats that provide adequate food supplies, especially following trans-Gulf flight. Our data further emphasize the need for understanding all aspects of stopover biology in order to adequately conserve migratory landbirds and their stopover sites.

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EFFECTS OF WINDOW ANGLING, FEEDER PLACEMENT, AND SCAVENGERS ON AVIAN MORTALITY AT PLATE GLASS

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ABSTRACT.—Extensive observations and experiments suggest that collisions with plate glass result in more avian mortalities than any other human-associated factor. We tested the effects of window angling and the distance of bird feeders from windows on bird-glass collisions. Strike frequency differed among windows oriented vertically (control) and those angled 20 and 40 degrees from vertical; as the angle of orientation increased, strikes and fatalities decreased. Strike frequency and fatalities at windows also increased as the distance between bird feeders and the glass surface increased. No fatalities were recorded when feeders were located within 1 m of a window, but a marked increase in mortality occurred when feeders were placed 5 and 10 m from the glass. Most glass-collision victims may go unnoticed, hidden by vegetation where they remain out of view or are removed by scavengers. We found that scavengers frequently removed baits from beneath windows at six buildings, but no baits were taken from a site without windows that served as a control. The importance of window strikes as an avian mortality factor, and the likelihood that it will increase over time, compel us to recommend a reevaluation of the Migratory Bird Treaty Act (MBTA). Angling panes in new and remodeled buildings and placing bird feeders closer to windows can potentially reduce avian mortality. *Received 3 September 2003, accepted 6 April 2004.*

Birds are vulnerable to collisions with windows—from small panes to walls of glass covering entire buildings (Klem 1989, 1991). Extensive observations and several experiments reveal that birds apparently cannot recognize clear or reflective panes of glass as barriers to be avoided (Klem 1990b). Conservative estimates of annual avian mortality from collisions with glass for the U.S. alone and for the entire North American continent range from approximately 100 million to 1 billion birds, respectively (Klem 1990b, 1991; Dunn 1993), representing from 0.5 to 5% of the fall bird population (American Ornithologists' Union 1975). Comparative figures for other human-associated bird mortalities (collisions with vehicles, communication towers, wind turbines, power lines, or nocturnal strikes at multistory buildings) are at least an order of

magnitude less than those known to occur at glass (Banks 1979, Klem 1991, Shire et al. 2000, Erickson et al. 2001, Johnson et al. 2002). Only predation by domestic cats—estimated at 1 billion birds per year in North America—results in comparable mortality rates.

Glass as a mortality factor for specific species is generally unknown. One exception is the Swift Parrot (*Lathamus discolor*) of Tasmania—1.5% of the entire population (1,000 breeding pairs) is killed annually by colliding with windows (R. Brereton pers. comm.). Lethal collisions have been recorded whenever and wherever both birds and glass occur. Moreover, the fittest individuals of populations are known to be as vulnerable as any other (Klem 1990b).

Although bird-glass collisions occur in every season, the general impression is that most occur during fall and spring migration. In fact, systematic monitoring of houses suggests that most birds in North America are killed during winter, when many are attracted to bird feeders (Klem 1990b, Dunn 1993). During 2001, 54 million U.S. residents (25% of the population ≥ 16 years of age) participated in feeding birds and other wildlife (U.S. Department of Interior and U.S. Department of Commerce 2002). Exacerbating our understanding of the problem is the practice of planting vegetation

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around human dwellings, which often hides glass-strike casualties from human attention (Klem 1990a). Scavengers are known to remove dead birds (Klem 1981), and they are believed to kill and remove injured birds from window-collision sites. However, no experiments have specifically addressed the removal of dead or injured birds by scavengers as a possible explanation for why collision casualties are not discovered beneath windows more often.

Here, we examine the effects of window angling on bird-glass collisions, and attempt to determine where bird feeders should be placed to reduce or eliminate window hazards. Additionally, we present experimental results that indicate scavengers regularly patrol areas near windows and remove evidence that avian fatalities have occurred.

METHODS

We conducted the window angling and bird feeder placement experiments at the 15-ha Muhlenberg College Raker field site south of Germansville, Lehigh County, Pennsylvania (40° 41' N, 75° 42' W). Land cover is 40% second-growth deciduous woodland, 35% fallow field, 15% wetland, 5% open water (Jordan Creek), and 5% man-made structures. The scavenger experiment was conducted at Muhlenberg College (40° 35' N, 75° 30' W) and Cedar Crest College (40° 35' N, 75° 31' W). The two campuses are adjacent to one another in suburban, west Allentown, Lehigh County, Pennsylvania.

Window angling experiment.—We conducted the window angling experiment from 20 January to 17 May 1991. The basic design was the same as reported previously (Klem 1989, 1990b), consisting of six wood-framed picture windows, simulating those in houses; all were placed in the same habitat and faced the same direction along the edge of a mixed deciduous forest and open field (Klem 1989: Fig. 1). Three of the windows were tinted dark gray and three were clear. Tinted panes alternated with clear panes across the six positions, which were separated from one another by 43, 15, 24, 18, and 20 m. Distances between windows were selected to simulate the construction practice of building homes in rows, in this case adjacent to one another along a tree line facing a field. The vegetation cover in the field

consisted of cut corn stalks and grasses, a uniform habitat with no obvious flight paths to attract birds to or away from the windows. Each window measured 1.4 m wide × 1.2 m high, and was mounted 1.2 m above ground. Wire-mesh trays were placed under each window to catch casualties. Tinted and clear windows were placed in each of three orientations: vertical (serving as the control), and angled downward from vertical at 20 and 40 degrees. Each window was constructed in such a way that it could be placed at all orientations. All panes remained in the same position throughout the experiment, and each day the three pane orientations were assigned randomly to the tinted and clear panes; panes were checked and changed 30 min before last light.

The parameter measured was the number of detectable bird strikes. A strike was registered when either a dead or injured bird was found beneath a window, or when fluid or a blood smear, feather, or body smudge was found on the glass. All window-killed casualties left evidence of a strike on the glass. Our data are likely to be incomplete and conservative because some strikes (e.g., a glancing blow) may not have left evidence of a collision. In addition, predators and scavengers may have removed some injured or dead birds that we did not detect.

Feeder placement experiments.—We conducted two feeder placement experiments, from 31 October to 17 December 1991 and from 24 January to 29 February 1992. The first experiment tested the effects of placing platform feeders 1, 5, and 10 m from conventional, vertically oriented panes. The second tested the effects of placing feeders 2, 3, and 4 m from windows. In the 1-, 5-, and 10-m experiment, we used the same six windows that were used in the angling experiment, but repositioned them so that they were 55 m apart. Each feeder placement was tested simultaneously at one clear and one tinted pane. Windows were positioned farther apart to reduce the possibility that birds attracted to one feeder placement might strike a window associated with another. In the 2-, 3-, and 4-m experiment, we replaced the tinted panes with clear panes because the quality of reflection from the tinted glass (salvaged) was not sharp, and we suspected that this effect contributed to the lower number of strikes at tinted panes

in our angling experiment. Each feeder placement was tested simultaneously at two clear panes. Bird feeders were flat trays measuring 30.5 × 61.0 cm, and placed so that they were centered and level with the bottom of each windowpane. Feed consisted of a 1:1 mixture of black-oil sunflower seeds and either cracked corn or white millet. Each feeder was lightly covered with the same feed mixture 1 hr before sunrise each day. We recorded strike frequencies in the same manner as in the angling experiment.

Scavenger experiment.—The scavenger experiment was conducted from 25 January to 10 April 1992. Seven locations, distributed among four buildings on the campuses of Muhlenberg and Cedar Crest colleges, were selected as experimental sites. Six of these sites were below windows at which lethal bird strikes were known to have occurred. A building wall without windows—but which faced habitat and had human passage similar to that of the other sites—served as a control. Approximately 30 g of chicken breast meat was used to simulate a window-killed bird approximately the size of a Hermit Thrush (*Catharus guttatus*). At each location bait was placed out of sight from human passersby. From 25 January to 8 March, baits at each site were checked every 12 hr (10:00 and 22:00 EST), and then once every 24 hr (22:00) from 9 March to 10 April. Baits were replaced after 4 days if no disturbance occurred, or during bait checks if baits had been removed or moved from their original location. The ground areas on which baits were placed were finely raked so as to record the tracks of potential scavengers. The parameter measured was the number of baits taken or moved from their original locations by scavengers each day at each site.

We used SPSS (SPSS, Inc. 2002) for all statistical analyses. Chi-square goodness-of-fit was used to evaluate experimental results except for one dichotomous comparison in which a 2-tailed binomial test was more appropriate. We considered test results to be statistically significant when $P < 0.05$.

RESULTS

Window angling experiment.—We recorded 53 strikes, of which 12 (23%) were fatal (Table 1). Dead birds included: Black-capped

TABLE 1. The number of bird strikes (fatalities) decreases with increased window angling. Data are from field experiments at Germansville, Lehigh County, Pennsylvania, 1991.

Glass type	Angle of tilt (orientation)			Total
	Vertical	20 degrees	40 degrees	
Tinted	9 (0)	6 (0)	2 (0)	17 (0)
Clear	21 (7)	9 (4)	6 (1)	36 (12)
Total	30 (7)	15 (4)	8 (1)	53 (12)

Chickadee (*Poecile atricapillus*), Northern Cardinal (*Cardinalis cardinalis*), White-throated Sparrow (*Zonotrichia albicollis*), Song Sparrow (*Melospiza melodia*), and Dark-eyed Junco (*Junco hyemalis*). Total number of strikes differed significantly across window angle, with 57% at the vertical control, 28% at the 20-degree angle, and 15% at the 40-degree angle ($\chi^2 = 14.3$, $df = 2$, $P = 0.001$). Similar strike differences occurred across window angle for both the clear panes ($\chi^2 = 10.5$, $df = 2$, $P = 0.005$) and tinted panes ($\chi^2 = 4.4$, $df = 2$, $P = 0.11$). Irrespective of window angle, strike frequency differed between clear (36) and tinted (17) panes (Binomial test, $Z = -2.47$, 2-tailed, $P = 0.013$).

Feeder placement experiments.—During the 1-, 5-, and 10-m experiment we recorded 105 strikes, 50% of which were fatal. Dead birds were: Blue Jay (*Cyanocitta cristata*), Black-capped Chickadee, Tufted Titmouse (*Baeolophus bicolor*), White-breasted Nuthatch (*Sitta carolinensis*), American Robin (*Turdus migratorius*), Common Yellowthroat (*Geothlypis trichas*), Northern Cardinal, White-throated Sparrow, Dark-eyed Junco, House Finch (*Carpodacus mexicanus*), and American Goldfinch (*Carduelis tristis*). Total number of strikes differed significantly across placements, with 25 (24%) at 1 m, 29 (28%) at 5 m, and 51 (48%) at 10 m ($\chi^2 = 11.2$, $df = 2$, $P = 0.004$). Fatal strikes also differed significantly across feeder placement, with 0 (0%) at 1 m, 17 (33%) at 5 m, and 35 (67%) at 10 m ($\chi^2 = 33.0$, $df = 2$, $P < 0.001$); all but four fatalities occurred at clear panes.

During the 2-, 3-, and 4-m experiment we recorded 197 strikes, 21 (11%) of which were fatal. Dead birds were: Tufted Titmouse, Northern Cardinal, Chipping Sparrow (*Spizel-*

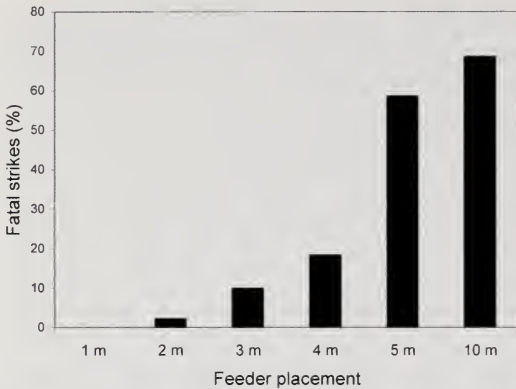


FIG. 1. The proportion of bird fatalities (%) at windows increases as bird feeders are placed farther from the glass surface. Data are from field experiments at Germansville, Lehigh County, Pennsylvania, 1991–1992.

la passerina), Field Sparrow (*S. pusilla*), White-throated Sparrow, Dark-eyed Junco, and House Finch. Total number of strikes differed significantly across placements, with 46 (23%) at 2 m, 91 (46%) at 3 m, and 60 (31%) at 4 m ($\chi^2 = 16.2$, $df = 2$, $P = 0.001$). The number of fatal strikes also differed significantly across feeder placement, with 1 (5%) at 2 m, 9 (43%) at 3 m, and 11 (52%) at 4 m ($\chi^2 = 8.0$, $df = 2$, $P = 0.018$). The combined results of both feeder placement experiments revealed a marked increase in the proportion of fatal strikes as distance between feeder and window increased (Fig. 1).

Scavenger experiment.—During 77 days, scavengers found and disturbed 69 (13%) of 539 baits. At the six sites below windows, the number of disturbed baits was 17, 12, 12, 8, 9, and 11, respectively. Tracks revealed that the following scavengers found bait: 15 (22%) squirrel, 31 (45%) cat, 3 (4%) dog, 4 (6%) bird spp., and 16 (23%) unidentified. Baits were found by the same type of scavenger at the same site on 6 (cat), 8 (cat), and 2 (squirrel and dog) consecutive days, suggesting that the same individuals may have returned to a location where food was found previously. At the control-site building with no windows there was no evidence that any scavenger discovered bait during the entire experimental period.

DISCUSSION

Preliminary observations had indicated that window angling might protect birds by reflect-

ing the ground instead of the surrounding habitat and sky (Klem 1990b). Our experiments revealed that window-strike fatalities can be reduced significantly if panes are angled downward 20° and 40° from the vertical. Angled glass also may reduce the force with which birds in horizontal flight strike panes. Although glass orientation does not eliminate the lethal hazard of windows, it is an effective bird-strike deterrent and should be considered by architects and others involved in planning new structures or in remodeling existing ones. The effectiveness of window angling is substantial and is likely to become practical in one-story structures or at ground level in multistory buildings.

Results of the angled window and feeder placement experiments in which tinted glass was used indicate that tinting may afford some protection for birds. Although fewer strikes were recorded at tinted panes, the numbers of strikes at tinted and clear windows had similar trends in the angling experiment. We believe that the lower number of strikes at our tinted panes is explained best by the relatively poor reflective quality of the salvaged glass we used. In a previous experiment, clear and tinted panes were equally lethal to birds (Klem 1989). However, the hazards of varying types of clear and tinted glass need further study to determine their specific risks.

Results of previous experiments have documented the effectiveness of two other methods in eliminating window kills, but these techniques are often unacceptable to home owners and managers of commercial buildings because they are costly, impractical, or aesthetically unpleasing (Klem 1990b, 1991). One method is to place a physical barrier (netting, awning) in front of glass to prevent bird strikes. Screens for this purpose are now commercially available. Another method is to apply opaque or translucent objects (hawk silhouettes, geometric shapes, other creative patterns), separated by 5–10 cm, to the outside surfaces of windowpanes (Klem 1990b). Objects of any shape that visibly contrast with glass allow birds to recognize and avoid windows. The use of ultraviolet (UV) patterns to deter bird-glass collisions is currently under study in our laboratory. The expected principal advantage of UV deterrents is that they will be invisible to humans. Another potential

long-term solution is the manufacture of a novel type of sheet glass, especially for multistory, glass-covered buildings (Klem 1991); this glass would provide an unobstructed view from the inside, but, when viewed from the outside, creative designs (dots, lines, variously shaped objects separated by 5–10 cm) would be visible to birds and direct them away from the hazard.

U.S. courts have established strict liability for unintentional avian mortality associated with pesticides and power lines pursuant to the Migratory Bird Treaty Act of 1918 (MBTA), as amended, or the Endangered Species Act (ESA) of 1973 (Corcoran 1999); however, the courts have not established strict liability for fatalities associated with vehicle, tower, or glass collisions. Our results suggest that bird kills at glass are substantial, foreseeable, and avoidable (Klem 1989, 1990b, 1991; Corcoran 1999) and we suggest that birds merit consideration for protection from glass collision under the purview of the MBTA and ESA.

Avian injury and mortality from collisions with glass can be reduced worldwide by those who feed birds. Our results showed an increase in window fatalities when bird feeders are placed 2–10 m from a glass surface, with marked increases at 5 and 10 m. Feeders placed within 1 m of a pane led to no fatalities and offer the most protection for birds, especially at residential buildings and visitor centers of local, state, and federal parks and other recreational facilities.

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REDISCOVERY OF THE SELVA CACIQUE (*CACICUS KOEPCKEAE*) IN SOUTHEASTERN PERU WITH NOTES ON HABITAT, VOICE, AND NEST

NATHANIEL G. GERHART^{1,2}

ABSTRACT.—Two new locations, vocalizations, and the nest of the little known Selva Cacique (*Cacicus koepckeae*, Icteridae) are described from southeastern Peru. Similarities between the vocalizations of Selva and Ecuadorian caciques (*C. sclateri*) indicate that the two species may be closely related. The Selva Cacique may be ecologically restricted to narrow rivers and headwater regions, where found in river margin habitats and nearby transitional forest. Its occurrence from an elevation of 300 m at the type locality to ≤ 575 m at the headwaters of the Río Manu Chico, 240 km from the type locality, indicates that it may occur in small numbers over a much larger area than was previously known. Received 29 July 2002, accepted 11 March 2004.

Until recently, the Selva Cacique (*Cacicus koepckeae*) was known from only two specimens collected at the type locality: Balta (10° 08' S, 71° 13' W; elevation 300 m), on the Río Curanja, Depto. Ucayali, Peru (Lowery and O'Neill 1965). Here, I report two new localities for the species in southeastern Peru, and provide the first description of its voice and nest.

STUDY AREA AND METHODS

Between 27 March and 20 April 1998, I observed 1–4 *C. koepckeae* seven times in the vicinity of the Nanti village of Montetoni (11° 54' S, 72° 21' W; elevation 550 m) on the upper Río Camisea, Depto. Cusco, and on the nearby Río Manu Chico, Depto. Madre de Dios, Peru (Fig. 1). On 1 October 1998, I observed a pair of birds near the Río Shihuaniro, a tributary of the Río Timpía, in the Matsigenka (Machiguenga) community of Timpía (12° 04' S, 72° 49' W; elevation 410 m) on the lower Río Urubamba, Depto. Cusco, Peru. I observed groups of 2–5 birds several times at this and other nearby sites on the Río Shihuaniro in Timpía on 23 October 1999, 16–17 May 2000, and 27–28 July 2001. All of these sightings were along narrow tributaries, but on 24 and 29 July 2001 I observed a pair of Selva Caciques visiting flowering *Erythrina* (Leguminosae) trees along the main course of the lower Río Urubamba across from the eco-tourism lodge of the Machiguenga Center for Tropical Studies in Timpía. I used a modified

Sony TCM-5000EV tape recorder and a Sennheiser short-shotgun microphone (model #ME66 with K6 powering module) to record vocalizations.

RESULTS AND DISCUSSION

Field identification.—*C. koepckeae* is distinctive, and its pattern of coloration—all black with a yellow rump—is striking. In this region of Peru, no other birds resemble it. The sympatric Yellow-rumped Cacique (*C. cela*) shows much more yellow on the rump, tail, and wings. Like *C. cela*, *C. koepckeae* has a light-colored bill and a bluish eye. The bill of *C. koepckeae* is grayish white and small for an icterid, imparting a small-headed look relative to the long, strong-headed appearance of *C. cela* (especially the male). *C. koepckeae* (23 cm) is slightly smaller than *C. cela* (23–29.5 cm; Ridgely and Tudor 1989).

Vocalizations.—On 11 April 1998, 09:00 EST, I made the first known recordings of *C. koepckeae* vocalizations near the Río Manu Chico, elevation 575 m, Manu National Park, just across the Isthmus of Fitzcarrald from the village of Montetoni on the upper Río Camisea (LNS #96000; see track 93 of Schulenberg et al. 2000). One bird vocalized while 3–4 individuals moved through the canopy of a predominantly *Cecropia* (Moraceae) riverine forest grove along an old, overgrown, dry river course. I recorded 20 sec of vocalizations before playback and 35 sec after playback.

The vocalization I recorded was a rapid series of loud, quick, explosive, paired notes: *chick-pouw*. In my analysis, each burst of sound constituted a note. Isler et al. (1998:

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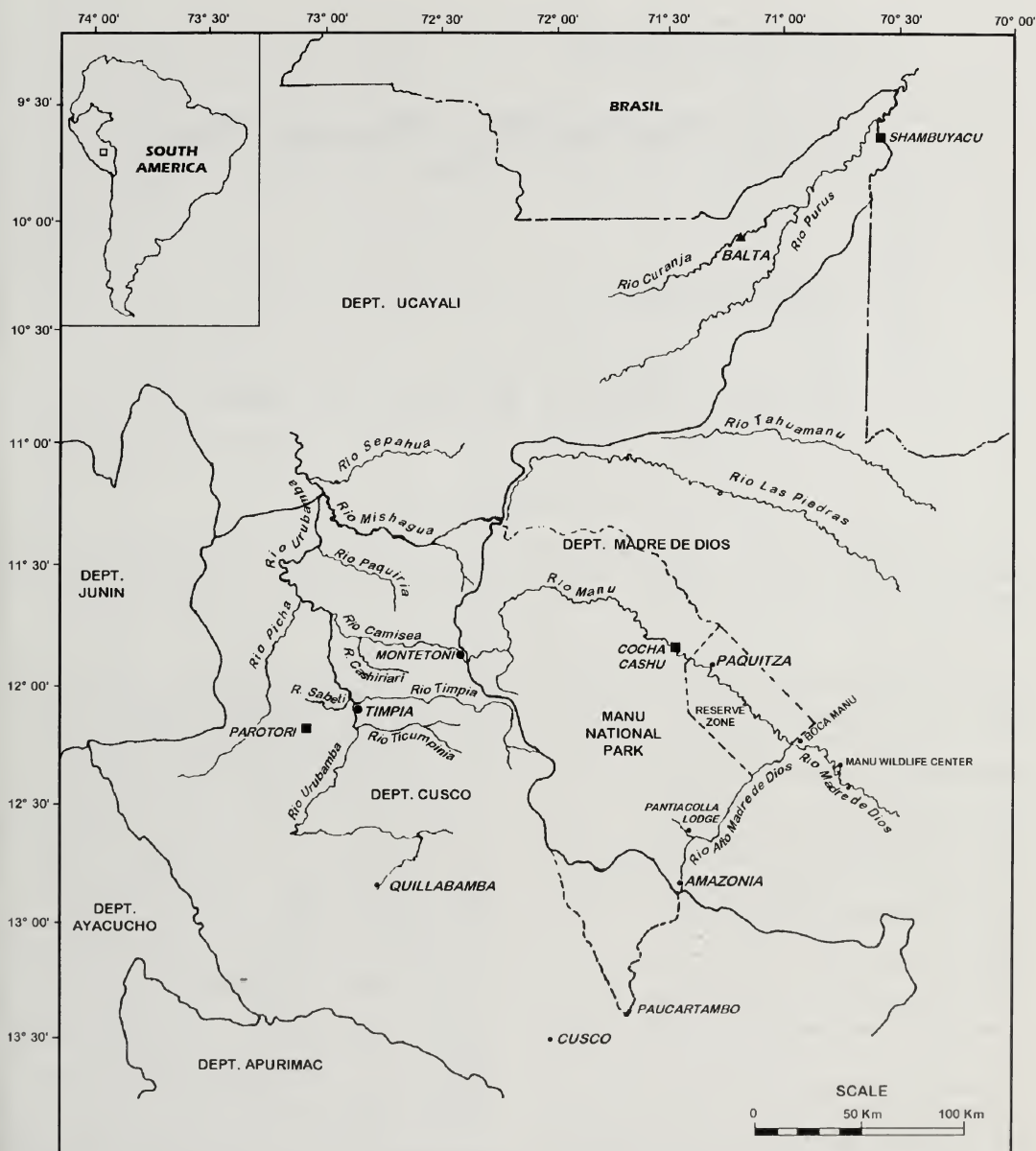


FIG. 1. Map of southeastern Peru showing the location of the type locality (Balta, solid triangle), the author's two new locations for *Cacicus koepckeae* (Montetoni and Timpia, solid circles), and other observers' recent encounters (Parotori, Cocha Cashu, and Shambuyacu, solid squares). Inset at upper left shows approximate location within Peru of the center of the enlarged map.

580) defined a note as "an unbroken trace on a spectrogram, including associated overtones." Paired notes were separated from each other by brief pauses and formed musical phrases, which may be repeated one or more times (Fig. 2). Before playback, the two-note phrases were given at about 1/sec for 20 sec

before the first noticeable pause. Following playback, the pace was slower—about one *chick-pouw* phrase every 2 sec for 35 sec. In both cases, the series began with 2–3 lone *chick* notes before the first two-note phrase. Before playback, several three-note *chick-pouw-pouw* phrases were interspersed in the

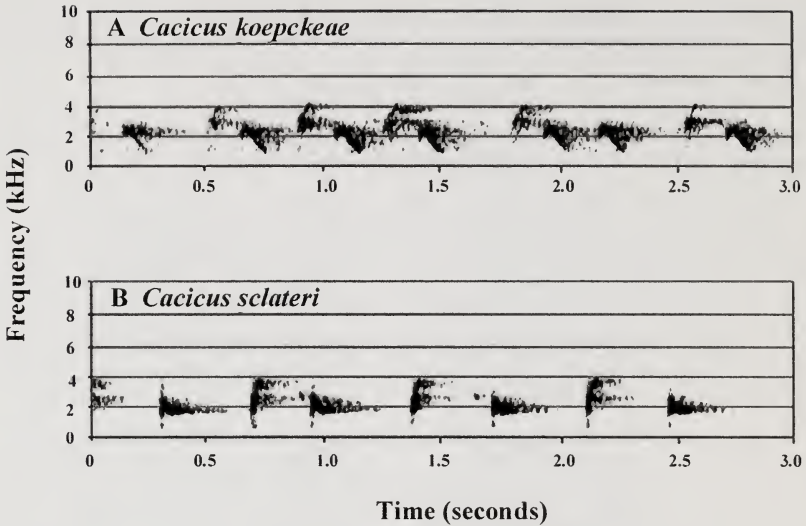


FIG. 2. Sound spectrograms of vocalizations of (A) *Cacicus koepckeae* (from the Río Manu Chico, south-eastern Peru; recorded before playback by N. Gerhart; LNS 96000) and (B) *Cacicus sclateri* (from the Kapawi Ecological Reserve, Río Pastaza, southeastern Ecuador; recorded before playback by J. Moore).

series of two-note phrases, but this only occurred once after playback.

On 1 October 1998, I recorded a pair on the Río Shihuaniro at about 09:00, when the birds vocalized from the canopy of river margin vegetation at a height of 5–8 m (LNS #96001). The rhythm of the vocalizations in this encounter was slightly different. Phrases were slower, more widely spaced, and not given in a long series: *chih-chih, pouw-pouw*. The sharp *chih* notes were given in quick succession, followed by a brief pause; the two *pouw* notes were given more slowly and less forcefully. One 14-sec sequence of the pair contained six phrases, with the birds loosely alternating phrases as they moved away. Only two of the six phrases were complete four-note phrases. Three shorter *chih-chih, pouw* phrases and one phrase with only the two loud, introductory notes were interspersed among the complete phrases. Long recordings (2 min 46 sec before playback and 29 sec after playback) of a single bird at a different site on the Río Shihuaniro on 17 May 2000 showed similar variations; at times, the cadence was similar to that in each of the original two recordings made in 1998.

These vocalizations of *C. koepckeae* are similar to one of the vocalizations of *C. sclateri*, the Ecuadorian Cacique, recorded by

Moore (1997) during September 1996 at Kapawi Lodge, Río Pastaza, in eastern Ecuador. Seven two-note *chick-kuh* phrases of *C. sclateri* were similar in pitch and quality to the *chick-pouw* phrase given by *C. koepckeae*. The first note of this *C. sclateri* vocalization is almost identical to the first note of *C. koepckeae*'s vocalization, with the second note only slightly shorter and sounding more clipped. The explosive quality and speed of the vocalizations of *C. sclateri* are also similar to those of *C. koepckeae*. Servat and Pearson (1991:94) described the vocalizations of *C. sclateri* as a "ringing song, peé-chur, peé-chur, peé-chur, chur-chur-chur."

Comparison of the last 2.5 sec of the sound spectrograms in Fig. 2 shows that *C. koepckeae* gives 11 notes, whereas *C. sclateri* gives 6. *C. koepckeae*'s pace is 4.4 notes/sec, whereas that of *C. sclateri* is 2.4 notes/sec. *C. koepckeae* changes the rhythm of its vocalization from a two- to a three-note phrase once during the series, whereas *C. sclateri* does not. Nevertheless, the basic two-note structure of both vocalizations is similar. Both vocalizations contain a steady and narrow range of frequencies. The F-shaped first note of both species is similar in shape and almost identical in frequency. The second note of the *C. koep-*

ckeae phrase is heavily down-slurred, giving it a longer, fuller, less clipped sound.

These vocal similarities suggest a close taxonomic relationship between *C. sclateri* and *C. koepckeae* (see below). The principal vocalizations of other caciques that could be closely related are substantially different from those of *C. koepckeae* and *C. sclateri*. For example, when not mimicking other species, *C. cela* typically gives a loud, variable four-syllable song beginning with a strong screech. *C. cela*'s frequent call note is a loud *tchak*. The Solitary Cacique (*C. solitarius*) gives a varied assortment of loud, whiney, squealing calls, but two of its most often-heard songs in southeastern Peru are (1) a series of low *whup* notes followed by a high *TEE-O*, and (2) a loud, piercing series of high *TEW* notes, sometimes preceded by a softer, low growl. The Southern Mountain-Cacique (*C. chrysonotus*; Ridgely and Greenfield 2001) gives a variety of loud, jay-like calls. Often one bird repeats these harsh notes while another duets with a descending whistle. The principal song of the Golden-winged Cacique (*C. chrysopterus*) is a high, loud *WHEEO* note, sometimes doubled, and preceded by several lower *glo-glo* notes. Its call is a catbird-like *wreyur* (Ridgely and Tudor 1989).

The vocalizations of *C. koepckeae* appear to lack the variability of those of *C. cela*, *C. solitarius*, and *C. chrysonotus*. The primary *chick-pouw* paired notes constituted all *C. koepckeae* vocalizations heard and recorded before 27–28 July 2001, when I recorded a different vocalization from one or both members of a pair disturbed by tape playback of the primary vocalization recorded along the upper Río Shihuaniro in Timpía. The new vocalization, reminiscent of some sounds made by *C. solitarius*, consisted of two consecutive mournful, downslurred, high-pitched whines, together lasting about 1.5 sec.

Habitat and behavior.—J. P. O'Neill (Ridgely and Tudor 1989:372) posited that *C. koepckeae* was likely "an arboreal bird occurring mostly at forest borders." T. A. Parker, III, reported that it "appears to be restricted to riverine habitats in the region" (Collar et al. 1992:961). My recent observations support those ideas. None of my encounters was far from river margin habitats, and the species

was never heard or seen inside continuous high ground, or *terra firme*, forest.

C. koepckeae's preferred habitat, at foothill elevations close to the eastern slope of the Peruvian Andes, is the transitional forest that lines narrow, high-gradient rivers such as the Ríos Shihuaniro, Manu Chico, and upper Camisea. In addition to the 17 sightings of *C. koepckeae*, I heard it 10 times without seeing it, for a total of 27 encounters. All 27 encounters were in river margin habitats, including *Gynerium* (Graminae) canebrakes, or in transitional forest near rivers. Nine of the 17 sightings of *C. koepckeae* (including almost all of the earliest sightings near Montetoni) have been of birds either perched in, or moving through, the canopy of river margin forest in areas where braided channels or dry river courses create a patchy distribution of river margin vegetation types. Six other sightings have been of pairs foraging along or flying across unbraided sections of the upper Ríos Camisea and Shihuaniro, plus two sightings of birds foraging in transitional forest along an unbraided (wider) portion of the lower Río Urubamba in Timpía.

The dry river courses, side branches, and braids (referred to as *otségoa* by local residents) of these narrow, high-gradient rivers carve up the river margin forests into a patchwork of successional habitats of varying ages and structures, forming the preferred habitat for *C. koepckeae*. The structure and distribution of *otségoa* habitat are spatially and temporally variable. Although these *otségoa* often fill during the rainy season and retain pools of standing water during the dry season, many are partially or fully overgrown with successional species such as *Cecropia*, *Balsa* (Bombacaceae), and *Gynerium*. In some cases, established groves of riverine forest shade an open understory scraped clean by rainy-season floods, but the understory can also be overgrown with dense, viney, rank vegetation.

In places, *otségoa* forests are similar in structure to the well-known primary successional habitats described from the Manu Biosphere Reserve area (Terborgh et al. 1984). Nevertheless, they are more heterogeneous and patchily distributed than the *Gynerium* canebrakes and transitional forest habitat types familiar to observers along the wider Manu and Madre de Dios rivers. *Otségoa* for-

ests seem to predominate at slightly higher elevations closer to the Andes, where *Ficus* (Moraceae), *Cedrela* (Meliaceae), and *Erythrina* species are less prominent members of the canopy tree community than in the transitional forests along lowland, meandering rivers, such as the middle and lower Manu. *Gynerium* cane is a common element in the understory of *otségoa* forests, and often forms isolated patches between rocky river beds; it does not tend to occur in the broader, more homogeneous stands referred to as the *zabolo* habitat type by Terborgh et al. (1984). In some places, patches of *Guadua* (Graminae) bamboo are also found in the understory of *otségoa* forests. *C. koepckeae* has been observed using these areas, even perching in bamboo, but it ranges throughout *otségoa* forests rather than being restricted to bamboo patches within them.

Four of the 17 sightings occurred 13–20 April 1998 at a *Gynerium*-dominated island in the middle of a dry river course (*otségoa*) on the upper Río Camisea, downstream of the village of Montetoni. In each encounter, a pair of birds flew to the island between 17:30 and 18:00 from the transitional forest that lined the dry river course and perched at the tip of the tallest *Balsa* sapling on the island before hopping down out of sight to roost. Playback of the vocalizations recorded on 11 April 1998 would sometimes draw one or both individuals across one arm of the dry river course, providing me with excellent views. Once they reached the island for the night, the pair did not vocalize more than once or twice, even in response to playback.

Between 06:50 and 07:04 on 23 October 1999 at the Río Shihuaniro in Timpía, I observed 1–5 individuals in four situations in the crowns of transitional river margin forest. This spot, where I also saw and recorded a pair of birds on 1 October 1998, is about 11 km up the Río Shihuaniro from the main population center of the Timpía community on the lower Río Urubamba. A single bird sunned and preened about 10 m above ground on top of a broken trunk that emerged from the rank vegetation of a small, partially overgrown side channel (*otségoa*) along the main river. Three more birds emerged, presumably from the dense undergrowth, and the four birds gathered 10 m above ground in the top of a tree

in the *otségoa* forest. They moved to the open crown of a 15- to 20-m-tall *Erythrina* tree that was just starting to leaf out, and appeared to probe along the bare branches from which hung some dry seed pods. They hopped between perches, staying mostly in the crown's outer branches. They then moved to a female (red) *Triplaris* (Polygonaceae) tree with drying, brown seed pods, about 15 m above ground. Five birds actively foraged in the clumps of dry pods by hanging in, and climbing through, the clumps. Because I made these observations with 10× binoculars from 50 to 150 m away, I could not determine whether the birds were taking insects or nectar, or probing in open seed pods. Nevertheless, they did not take fruit from an adjacent tree.

During the early morning hours of 28 July 2001, on the upper Río Shihuaniro, I observed repeatedly a pair of *C. koepckeae* visiting a flowering *Erythrina* tree to take nectar. In each of several visits, the birds would arrive together, visit clumps of flowers mostly in the outer branches, and never stay more than a few minutes. On 24 and 29 July 2001, at 16:15 and 15:00, respectively, I observed a pair of *C. koepckeae* foraging in a group of *Erythrina* trees in full bloom, alongside the main course of the lower Urubamba River. Heard and seen on both occasions on the bank opposite from the ecotourism lodge of the Machiguenga Center for Tropical Studies, the pair took nectar from several trees before moving on. They did not linger in any one tree as *C. cela* and other large icterids often do in *Erythrina* trees in full bloom. Although the species is largely restricted to narrower rivers and headwater regions, my two sightings along the main course of the lower Río Urubamba indicate that *C. koepckeae* may visit other transitional and riverine forest habitats opportunistically to take advantage of seasonally available nectar resources, especially rich patches of flowering *Erythrina* trees.

My observations from the Río Shihuaniro suggest that pairs or family groups of *C. koepckeae* start their morning foraging slowly, sunning and preening, and then become more active, and perhaps more vocal, as they move to denser vegetation. My experiences with birds heard along the Río Shihuaniro indicate that response to playback is variable at short range and minimal at long range. A pair re-

sponding to close playback on the Río Shihuaniro on 16 May 2000 remained silent, but readily moved across the river twice, perching in the open 4–15 m above ground in the crowns of riverside trees and bamboo. At the same spot on 27 July 2001, what was presumably the same pair also drew nearer and then crossed the river several times in response to playback. The pair had been actively vocalizing when encountered, and responded to playback with a series of *chick-pouw* vocalizations, eventually giving the disturbed vocalization and a rapid series of *chih-chih-pouw-pouw* phrases after repeated playback.

It appears that foraging pairs or small groups of birds range through the canopy of transitional forest throughout the middle of the day, with foraging concentrated in the early morning and late afternoon. In my experience, *C. koepckeae* moves rather steadily through its preferred habitat, vocalizing only occasionally. In one case, it roosted with colonial icterids, such as Olive Oropendola (*Psarocolius yuracares*), Russet-backed Oropendola (*P. angustifrons*), and Crested Oropendola (*P. decumanus*). A Matsigenka resident of Timpía noted that *C. koepckeae* seasonally fed at the white flowers of an *Inga* sp. (Leguminosae) growing near the Río Shihuaniro. *C. koepckeae* should be looked for around the patchily concentrated nectar resources such as *Erythrina* and *Inga* trees, and possibly *Mucuna* sp. (Leguminosae) vines, which are visited by other icterids.

Nest.—On 28 July 2001, along a braided section of the upper Río Shihuaniro, I observed an active nest of *C. koepckeae* for about an hour. The solitary nest was hanging from the tip of one of the lowest branches, 15–18 m above ground in a mature, 28- to 30-m-tall *Erythrina* tree growing within 10 m of the river bank. I estimated the nest to be 50–70 cm in length. It resembled the pendant nest of *P. angustifrons*, but appeared shorter and slimmer. It was constructed of woven plant fibers that formed a tear-drop shape, had a top entrance, and hung from a long, thin “tail” like the nest of *P. angustifrons*. A (presumably) adult *C. koepckeae* came to the nest about every 5 min, but in one instance it made as many as three visits in a 6-min period. I could not tell what it was bringing to the nest, but each time it entered the nest it stayed in-

side the chamber for 5–70 sec. Several Crested Oropendolas were building nests on the other side of the same tree.

On 16 May 2000, at separate sites along the Río Shihuaniro, I observed two old, inactive nests of similar shape and dimensions that were reported by a local resident to be nests of *C. koepckeae*. Each nest was situated 5–6 m above ground in 12- to 15-m-tall trees, hanging near the end of a branchlet off a main lateral branch. The trees were within 5 m of the river bank, and one nest almost hung over the water. In each case, as with the active nest, the tree’s crown stood alone, away from other crowns. At all three sites, transitional forest with a broken canopy lined the Río Shihuaniro. At two of the sites, the understory was a dense, young stand of *Guadua* bamboo. A local resident said that *C. koepckeae* never nested in colonies with the oropendolas or with *C. cela*, but that it nested at around the same time of year (during the June to November dry season).

Taxonomic relationships.—Although precise relationships within this genus are not known (Lanyon and Omland 1999), similarities in vocalizations, habitat, and behavior support the hypothesis that *C. koepckeae* and *C. sclateri* are closely related, considered by some to be “sister species” (T. A. Parker in Cardiff and Remsen 1994). In addition to its vocal similarities, the all-black *C. sclateri* is also almost identical to *C. koepckeae* in size and morphological structure, and it has a similar lowland Amazonian distribution (Cardiff and Remsen 1994). Based primarily on plumage characteristics, Lowery and O’Neill (1965) originally proposed that *C. chrysopterus* was *C. koepckeae*’s closest relative; structural differences in the tail, feet, and bill were mentioned but not considered diagnostic. J. P. O’Neill (Jaramillo and Burke 1999) now considers this early idea to be in error. Other black and yellow caciques that could be closely related include the similarly plumaged *C. chrysonotus*, which occurs in temperate Andean forest in southeastern Peru (principally at 1,800–3,000 m); *C. chrysonotus*, however, is much larger, and, like *C. chrysopterus*, differs in habits and voice (Ridgely and Tudor 1989). *C. cela* differs in size, plumage, voice, and has a colonial social system.

Other factors such as foraging behavior and

habitat preference also can be considered in determining species' relatedness (Remsen and Schulenberg 1997). Similarities in habitat use and foraging behavior of *C. sclateri* and *C. koepckeae* support their close relationship. Both are primarily arboreal foragers and occur in similar transitional forest or forest edges near water. Like *C. koepckeae*, *C. sclateri* forages in middle and upper levels of flood-plain forest (Ridgely and Tudor 1989, Servat and Pearson 1991). In one case, *C. sclateri* foraged actively for nectar or insects at flowers 4–10 m above ground in a leguminous tree alongside the Samiria River (Servat and Pearson 1991). J. P. O'Neill (pers. comm.) observed a pair of birds foraging "4–5 m up in *Gynerium* and *Cecropia* at the edge of an Aguaruna-Jivaro garden plot near the edge of the [Cenepa] river." Ridgely and Tudor (1989: 368) classify *C. sclateri* as "apparently rare in canopy and middle levels of forest borders and woodland," where birds foraged in pairs, "well up in trees, often probing into epiphytes and the bases of leaves." Despite these similarities, vocal differences (especially the structural difference of the second note of their primary vocalizations) do not support the suggestion that *C. koepckeae* and *C. sclateri* could be subspecies of one species (cf. Jaramillo and Burke 1999).

Distribution and conservation.—Based on my observations, *C. koepckeae* may be ecologically restricted to narrow rivers, such as those found in headwater regions at foothill elevations close to the eastern slope of the Peruvian Andes. This seems especially evident in the Timpía sightings. Before the sightings of 24 and 29 July 2001, 8 months of fieldwork (spread over 3 years) along the main stem of the Río Urubamba had resulted in no records of *C. koepckeae*. Over this same time period, less than 15 km away, I recorded *C. koepckeae* on 8 of the 11 days I spent up the narrow Río Shihuaniro. In Timpía, the conventional wisdom among community members about *C. koepckeae* (known as *pichócho* in the lower Urubamba dialect of the Matsigenka language) is that it is rarely, if ever, seen down as far as the main course of the lower Río Urubamba.

Between the type locality and the sites of my recent observations, *C. koepckeae* has now been recorded between 300 and 575 m ele-

vation in southeastern Peru. The range or habitat requirements of *C. koepckeae* must be somewhat restricted because, until recent sightings (see below), it had not been observed at the several heavily studied sites in Depto. Madre de Dios (although there were several possible sightings during the 1980s in the Manu National Park area; Collar et al. 1992). Other narrow rivers at similar elevations in the region—for example, the headwaters of the Ríos Alto Manu, Serjali, Paquiría, Mishagua, Cashpajali, Sepahua, Las Piedras, Cujar, Alto Púrus, and Curanja—and possibly those in western Brazil, could provide habitat for *C. koepckeae*.

Based on its habitat requirements, one would expect *C. koepckeae* to occur in the eastern part of the Manu Biosphere Reserve in Depto. Madre de Dios, where appropriate habitat may exist away from the main river. It likely occurs in small numbers at least as far southeast as Boca Manu (12° 15' S, 70° 50' W), where a possible sighting was reported in 1983 (Collar et al. 1992; M. Kessler pers. comm.). Although not particularly well documented, this sighting, along an old branch of the Río Manu, would represent a significant range extension to the east and south of the three confirmed sites discussed in this paper.

Several other recent encounters add to our knowledge of the distribution and ecology of *C. koepckeae*. A specimen of *C. koepckeae*, only the third of its kind, was collected along the pipeline route of the Camisea gas project in Parotori, Depto. Cusco, about 25 km west of Timpía in the upper Río Picha drainage (I. Franke pers. comm.). During September 2001, near the Cocha Cashu Biological Station (11° 51' S, 71° 19' W; elevation ~380 m) in Manu National Park, J. Tobias (pers. comm.) repeatedly observed and tape recorded foraging groups of *C. koepckeae* along a bamboo-lined stream near a site known as Playa Bonita, about 8 km inland from the main stem of the Manu River. During June 2000, P. Hocking (pers. comm.) reported seeing a *C. koepckeae* fly from a "very long" nest along the Río Shambuyacu (a tributary of the Río Púrus), Depto. Ucayali, near the Brazilian border (i.e., relatively near the type locality at Balta). Most significantly, in 1996 D. Lane (pers. comm.) reported having seen a possible *C. koepckeae* near Cushabatay in Depto. Ucayali, several

hundred km from the sites mentioned in this paper. Indeed, if *C. koepckeae* and *C. sclateri* form a superspecies (as suggested by J. P. O'Neill in Jaramillo and Burke 1999), then *C. koepckeae* could occur well north into east-central Peru.

The September 2001 sightings documented with tape recordings from Manu National Park (J. Tobias pers. comm.) offer hope that more will soon be discovered about the ecology of this little-known species. J. Tobias (pers. comm.) reported that three different family groups of *C. koepckeae* (of four, five, and six individuals, respectively) were readily observable along a stream 4–8 m wide in lowland rainforest. During eight visits along a 5-km stretch of the stream over a 4-week period, Tobias recorded the species 17 times, with each family group tending to be found repeatedly along the same stretch of stream. Tobias reported that during 2 months of intensive fieldwork in the surrounding mature, floodplain forest, he never encountered *C. koepckeae* away from the stream: "They were always along the stream itself, never in adjacent forest, and appeared to be restricted to disturbed riverine regrowth containing cane, bamboo, dense creepers, and some *Heliconia* [Heliconiaceae]... They ranged from the low understory to the upper canopy, but spent most time 1–5 m above the ground in dense tangles of bamboo or vines. The species was almost always located by its loud and distinctive vocalizations... The species is not so much skulking as inconspicuous and highly local." These observations support my hypothesis that *C. koepckeae* is ecologically restricted to narrower rivers and the patchy, successional habitats along their margins.

Further research is needed on the foraging ecology and distribution of *C. koepckeae* before its conservation status can be assessed. I have seen and heard it several times near human habitation, where a mosaic of cultivated areas dominated the transitional forest near the river edge. The pattern of low-impact, small-scale agriculture practiced by the indigenous peoples of the lower Río Urubamba region does not seem to be incompatible with the ecological needs of *C. koepckeae*. Most riverine habitats in the aforementioned headwaters regions are still intact, and the Manu Biosphere Reserve and the contiguous indig-

enous reserve to the west of the park may afford the species some de facto protection. Nevertheless, current and proposed petrochemical development in the Camisea and Río de Las Piedras areas may threaten the long-term integrity of *C. koepckeae* habitat in those areas. The conservation measures proposed by Collar et al. (1992:961) for this little-known species state that the first requirement is the identification of "general areas in which some reasonable population exists." My observations have begun to do that, but further exploration is necessary to document more fully the distribution and ecological requirements of *C. koepckeae*.

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DIVING BEHAVIOR AND FORAGING AREAS OF THE NEOTROPIC CORMORANT AT A MARINE COLONY IN PATAGONIA, ARGENTINA

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ALEJANDRO GATTO,³ AND GASPAR SORIA⁴

ABSTRACT.—The Neotropic Cormorant (*Phalacrocorax brasilianus*) is a widespread and abundant species distributed throughout the Neotropics. We report on diving behavior and foraging areas of Neotropic Cormorants in inshore marine waters of Patagonia, Argentina. Mean dive duration was 18.9 ± 5.3 sec and differed significantly among birds. Maximum dive duration was 43 sec. Birds spent 58–79% of their time at sea underwater. Mean recovery time at the surface between successive dives was 6.7 ± 1.5 sec, and was also significantly different among individuals. Mean diving efficiency (mean dive duration time/mean recovery time) was 2.6 ± 0.5 (range: 0.5–4.6). We were able to locate birds while feeding on 112 of 215 occasions. Almost 90% of mapped locations (68 feeding trips) were within 2.5 km of the colony. However, we did not receive a signal on 103 occasions, suggesting that foraging may also occur in waters outside the inlet where the colony was located. High variability in dive duration and recovery time is congruent with flexible foraging techniques and diet, as Neotropic Cormorants feed on both bottom and pelagic schooling fish. Received 8 July 2003, accepted 26 March 2004.

The Neotropic Cormorant (*Phalacrocorax brasilianus*), is widely distributed in the Neotropics. The species ranges from the southern United States to Cape Horn at the southern extreme of South America (Orta 1992, Telfair and Morrison 1995). Neotropic Cormorants are one of the few cormorant species that occupy both freshwater and marine environments, breeding in inland wetlands, fast-flowing rivers, high-altitude lakes, and on marine shores and islands (Orta 1992). Like other cormorants and shags (see Johnsgard 1993 for a review), they are foot-propelled pursuit-divers, although they can feed by plunge-diving under special sea conditions (Duffy et al. 1986, Humphrey and Rasmussen 1988).

In Argentina, the Neotropic Cormorant is a widespread and abundant species, with colonies reaching up to several thousand individuals at some wetlands in northern and central

Argentina (De la Peña 1980, Navas 1993). On the marine coasts of Patagonia, it breeds at twelve sites with a total breeding population estimated at 1,200 pairs (Yorio et al. 1999). Despite its abundance and broad distribution, the Neotropic Cormorant has been little studied throughout its range (Telfair and Morrison 1995). In Argentina, general aspects of its breeding biology and behavior have been described for freshwater populations (Bo 1956, Daneri 1960, Aramburu and Bo 1961, De la Peña 1980, Mosqueira et al. 1987) but relatively little has been published on marine populations (Yorio et al. 1994, Quintana et al. 2002b). To date, there is little information on the feeding ecology of the Neotropic Cormorant, and no available data on diving parameters of birds feeding in freshwater or marine environments. Here, we report on the diving behavior and use of foraging areas of this species in inshore marine waters of Patagonia, Argentina.

METHODS

During the 2001 breeding season, we studied the diving behavior and determined the feeding areas of the Neotropic Cormorant at a colony of 120 breeding pairs at Isla Vernaci Sudoeste, Caleta Malaspina ($45^{\circ} 11' S$, $66^{\circ} 30' W$), Chubut, Argentina (Fig. 1). This island complex is located at the mouth of an inlet (35 km²; Herrera 1997) where 9 of 16 seabird

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FIG. 1. Foraging locations and density contours (resulting from kernel estimation of locations) for Neotropic Cormorants breeding at Isla Vernaci Sudoeste (Caleta Malaspina, Argentina), 2001. Contours encompass 50, 75, and 95% of locations.

species that breed along the Argentine Patagonian coast have colonies (Yorio et al. 1998).

A VHF radio transmitter (Standard model, Advanced Telemetry Systems, Bethel, MN) was attached to eight adult birds during the late incubation period (29 November). Radios were fixed to the two central tail feathers using waterproof tape (Wanless et al. 1998). The procedure was completed in less than 5 min and the released birds flew directly to sea before returning to their nests. Mean weight of radios was 18.4 g (SD = 0.2, $n = 6$), approximately 1% of adult body mass (mean = 1.65 kg, SD = 0.2, $n = 8$ birds). Transmitters did not appear to affect cormorant breeding and feeding activities.

Radio signals were monitored from 11 tracking stations separated by 0.7–9.3 km, located on shore at 10–50 m above sea-level.

Receivers were single channel (R161A model, Advanced Telemetry Systems, MN) connected to hand held 3-element Yagi aerials (Advanced Telemetry Systems). Radio signals disappeared when birds were underwater and resumed when cormorants resurfaced. It was therefore possible to identify a sequence of dives as a series of regular breaks in the signal (see Wanless et al. 1991). Dive duration corresponded to the time interval over which the signal was interrupted and recovery times (the interval at the surface between successive dives) to the time during which a signal was audible. Dive efficiency was defined as the ratio between mean dive duration and mean recovery time (Dewar 1924). Birds were radio-tracked throughout daylight hours between 29 November and 3 December 2001.

Birds were treated individually because dif-

TABLE 1. Dive parameters of Neotropic Cormorants at Caleta Malaspina, Argentina, during the 2001 breeding season.

Bird	Number of dives	Trips recorded	Mean dive duration (sec) \pm SD	Maximum dive duration (sec)	Mean recovery time ^a (sec) \pm SD	% time underwater \pm SD
14	213	4	15.2 \pm 6.9	33	5.0 \pm 2.3	69.2 \pm 9.2
54	113	2	16.9 \pm 4.1	28	6.2 \pm 2.2	72.6 \pm 3.6
104	6	1	22.8 \pm 7.0	30	9.8 \pm 1.2	69.9
133	251	5	15.9 \pm 8.5	35	6.5 \pm 4.0	58.4 \pm 17.7
143	95	2	13.4 \pm 8.2	30	5.5 \pm 3.5	70.2 \pm 3.7
153	176	5	28.6 \pm 8.9	43	7.1 \pm 2.4	79.4 \pm 4.4
163	65	1	19.3 \pm 6.1	32	6.8 \pm 2.5	71.5
Total	919	20				
Mean \pm SD			18.9 \pm 5.3		6.7 \pm 1.5	70.2 \pm 6.2

^a Excludes recovery times >20 sec.

ferences between birds were significant (one-way ANOVA, $P < 0.05$). Means of diving parameters were determined for each individual and then pooled to calculate overall mean values. The use of non-independent observations is valid if the replicates are pooled to estimate a mean value (Hurlbert 1984).

Feeding areas were defined as the locations where birds dived repeatedly; these were estimated by triangulation from the direction of the radio signals. During feeding trips, and while birds were at the surface between consecutive dives, at least two stations simultaneously recorded the direction of the most stable and strongest signal. Observers at the two tracking stations were in radio contact. To control for errors, an observer with binoculars and a hand-held aerial checked a sample of positions. We used kernel density estimates to

characterize the spatial distribution of feeding locations following Wood et al. (2000). We defined three categories of activity ranges as the areas encompassing 95, 75, and 50% of locations at sea.

RESULTS

Diving behavior.—We recorded 919 dives from seven incubating birds during 20 feeding trips (Table 1). We were unable to obtain data from one of the eight instrumented birds due to radio failure. Mean dive duration was 18.9 sec (SD = 5.3, $n = 7$ birds; Table 1) and modal dive duration was 15–20 sec. Only 3% of the dives ($n = 919$) were longer than 35 sec (Fig. 2). Maximum dive duration was 43 sec and birds spent between 58 and 79% of their time at sea underwater (Table 1). Dive duration differed among individuals (Kruskal-Wallis $H = 252.5$, $n = 887$, $P < 0.001$). Recovery time, excluding prolonged surface intervals (PSI) longer than 20 sec, was 6.7 sec (SD = 1.5, $n = 7$ birds; Table 1). PSIs ranged from 21 to 199 sec and were infrequent (3% of total surface intervals). Recovery time differed among individuals (Kruskal-Wallis $H = 72.3$, $n = 871$, $P < 0.001$). Mean diving efficiency was 2.6 ± 0.5 ($n = 6$ birds). The correlation between dive duration and subsequent recovery time was low ($r^2 = 0.0003$, $n = 892$, $P > 0.05$). Recovery time increased linearly with duration of the previous dive (Recovery time = $7.0 + 0.02 \times$ Dive duration) but the slope was low and non-significant ($t_{890} = 0.5$, $P > 0.05$).

Both dive duration and recovery time differed among trips for three birds, while only

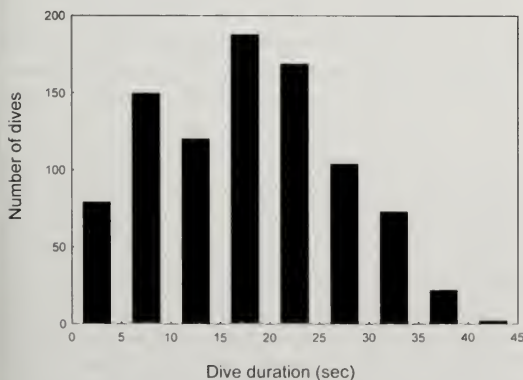


FIG. 2. Frequency distribution of dive durations ($n = 919$ dives) for Neotropic Cormorants at Caleta Malaspina, Argentina, 2001, during the late incubation period.

one (either dive duration or recovery time) differed for two other birds (Kruskal-Wallis and Mann-Whitney U -tests, $H > 14$ and $Z > 3.5$, $n = 94$ –236 dives per bird, all $P < 0.05$). We excluded two birds (nos. 104 and 163) from the analysis, as only one trip was recorded for each of these birds.

In a diving sequence, the birds performed a general pattern of immersions longer than the intervals on the surface, except for one trip of bird no. 133. Time underwater during foraging trips varied from 31 to 84% of the time at sea, but in 60% of the trips ($n = 20$) the birds foraged underwater more than 70% of the time. Within a feeding trip, dive duration and recovery time were variable, with CV ranging from 13 to 54% and 20 to 252% for dive duration and recovery time, respectively.

Foraging areas.—Both telemetry and observational data indicated that Neotropic Cormorants from Isla Vernaci Sudoeste fed in inshore and shallow waters (<1.3 km from the coast and <10 m depth) both inside and outside the inlet. We were able to locate birds while feeding inside the inlet on 112 occasions (52%, $n = 215$). However, we did not receive a signal on 103 occasions (48%, $n = 215$) while the birds were absent from the colony. Both tagged and untagged individuals were observed outside the inlet diving in inshore waters in small bays located at both sides of its mouth.

Inside the inlet, 71 feeding areas were identified by means of radio telemetry for 68 foraging trips (three foraging trips included two locations; Fig. 1). We also observed four of the eight instrumented birds feeding inside the inlet on a total of six occasions (Fig. 1). Eighty seven percent of mapped locations ($n = 71$) were within 2.5 km of the colony, near the mouth of the inlet (Fig. 1). During a single trip, cormorants almost invariably used the same foraging area; on only 2 of the 68 trips did the birds change foraging sites.

DISCUSSION

Diving behavior.—Our study presents the first description of the diving behavior of the Neotropic Cormorant in marine waters. Our results show that Neotropic Cormorants dive near the coast in shallow waters. The diving pattern consisted of extremely short dives not exceeding 20 sec in 97% of the recorded

dives, followed by short intervals at the surface. Morrison et al. (1978) reported a similar diving pattern for adult Neotropic Cormorants foraging in a freshwater pond in Texas, USA. Diving durations and recovery times of the Neotropic Cormorant were markedly shorter than those of Rock Shags (*Phalacrocorax magellanicus*) and Imperial Cormorants (*Phalacrocorax atriceps*) breeding in the same study area. Neotropic Cormorants performed shorter dives (18.9 sec compared to 47.2 and 94.8 sec for Rock Shags and Imperial Cormorants, respectively) and spent shorter intervals at the surface (6.7 sec compared to 15.5 and 163.6 sec for the Rock Shag and Imperial Cormorant, respectively) (Quintana 1999, Quintana et al. 2002a, Sapoznikow and Quintana 2003; FQ unpubl. data).

While Rock Shags and Imperial Cormorants show a diving pattern that is characteristic of bottom feeders (Quintana 1999, Quintana et al. 2002a, Sapoznikow and Quintana 2003; FQ unpubl. data), the Neotropic Cormorant shows a more flexible diving strategy. Wilson and Wilson (1988) suggested that besides physiological constraints related to body mass, differences in diving behavior could reflect variation in features of foraging areas such as bathymetry, bottom topography, water turbidity, and type and/or availability of prey. Because our data from Rock Shags and Imperial Cormorants also come from adult birds feeding within Caleta Malaspina during the same part of the season, differences in environmental characteristics of foraging areas do not seem to be a plausible explanation for differences in diving behavior. Rather, differences in diving depths, foraging techniques, and diet may best explain dissimilar diving patterns found among these three sympatric species.

In our study area, Neotropic Cormorants have been observed foraging individually as well as in flocks (FQ pers. obs.); Imperial Cormorants seldom engage in group foraging and Rock Shags always forage alone (Quintana et al. 2002a, Punta et al. 2003). In addition, even when pursuit diving appears to be the usual feeding behavior, Neotropic Cormorants have been observed foraging in flocks by plunging in very shallow and coastal waters (Duffy et al. 1986, Humphrey and Rasmussen 1988; FQ pers. obs.). Similar foraging tech-

niques for Neotropic Cormorants also have been observed in Puerto Deseado, Santa Cruz, Argentina (P. A. Gandini and E. Frere pers. comm.). In accordance with the more flexible foraging strategy shown by Neotropic Cormorants in our study area, preliminary data suggest that their diet includes a higher proportion of surface-schooling fish than that of the other two cormorant species (Malacalza et al. 1994, 1997; Gosztonyi and Kuba 1998; Punta et al. 2003; FQ and PY unpubl. data). The high within-trip variability in dive duration and recovery time found in Neotropic Cormorants in this study is congruent with their flexible foraging techniques and diet. In Caleta Malaspina, Neotropic Cormorants appear to spend time searching for sheltered, but predictable, bottom-dwelling prey as well as pelagic schooling fish when they occur in the area. This probably results in the variability in their diving parameters. A theoretical model developed by Grémillet and Wilson (1999) for the Great Cormorant (*Phalacrocorax carbo*) predicts that cormorant diving parameters are most strongly influenced by prey availability.

Foraging areas.—Neotropic Cormorants often foraged within Caleta Malaspina in an area close to the colony at the mouth of the inlet. We did not detect radio signals almost half of the time birds were absent from the colony, suggesting that the cormorants also regularly forage outside the inlet. In some of these cases, however, birds may have been feeding in areas behind islands or in small bays hidden behind elevated terrain, which interfered with signal transmission. This was confirmed in several cases through direct observation of tagged individuals and simultaneous radio-tracking. Observations along the outer coasts of the inlet revealed that birds forage in inshore waters of small bays.

Foraging activity was concentrated in specific coastal sections of Caleta Malaspina, mostly at the mouth of the inlet; we rarely observed foraging at the inland end of the inlet. Birds there generally foraged in mixed feeding flocks, likely taking advantage of pelagic prey which had moved into that part of the inlet. Neotropic Cormorants also regularly occur in association with the commercial harvesting activities of macroalgae, as the harvesting sledge stirs the ocean bottom and likely makes bottom fishes more accessible to the

birds (H. Hernández pers. comm.). This and other activities, such as mariculture and occasional guano harvesting from Imperial Cormorant colonies, also likely affect the foraging behavior and spatial distribution of Neotropic Cormorants. Our study on foraging patterns and locations should help in the definition of spatial and temporal harvest zoning schemes and help prevent modification of key feeding habitats.

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PHENOLOGY, HABITAT USE, AND NESTING OF THE RED-BREASTED CHAT (*GRANATELLUS VENUSTUS*)

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ABSTRACT.—From March 1999 to August 2000, we conducted monthly mist netting in the Chamela-Cuixmala Biosphere Reserve, Jalisco, Mexico to document the phenology and habitat use of the Red-breasted Chat (*Granatellus venustus*). We collected information on its nesting biology during the breeding season of 2001. Chats ($n = 116$) were caught throughout the 18 months of the study; however, far fewer captures occurred during the dry season than during the wet season. Our capture data revealed that chats made greater use of deciduous ($n = 88$) than semi-deciduous forest ($n = 28$); there were no interactions among forest type, season, and gender. Birds in breeding condition were captured June–September and molting birds were captured August–October. We found 10 cup-shaped nests in June and July. Nests were 48–103 cm above ground in saplings ≤ 2 m high. Clutch size was 3–4 and only the female incubated. The incubation period was 14 days, and we estimated the nestling period to be approximately 8–10 days. Of eight nests found with eggs or young, three were depredated during the egg stage, three during the nestling stage, and two were successful. Received 29 June 2003, accepted 18 March 2004.

The New World genus *Granatellus* includes three species that occur in southwestern Mexico (Red-breasted Chat, *Granatellus venustus*), southern Mexico and northeastern Central America (Gray-throated Chat, *G. sallaei*), and the Amazonian lowlands of South America (Rose-breasted Chat, *G. pelzelni*) (Sibley and Monroe 1990). The conservation significance of these species is high because of their relatively restricted range, but virtually no details of their life history are known. Also, the systematic position of the genus is uncertain (Lovette and Bermingham 2002). There is only one description of a nest of the *francescae* group of *G. venustus* from the Tres Marias Islands (Grant 1964), and a recent description of two nests of Gray-throated Chats (Salgado-Ortiz et al. 2001).

The Red-breasted Chat is endemic to the tropical deciduous and semi-deciduous forest of western Mexico from northern Sinaloa south to Chiapas (American Ornithologists' Union 1983). Schaldach (1963:81) included Red-breasted Chats "among the rarest birds of the Pacific slope of Mexico"; Alvarez del Toro (1980) described them as uncommon in Chiapas and Ornelas et al. (1993) observed

chats only twice during 2 years of work in the region of Chamela, Jalisco. Its relatively limited distribution, the lack of information on its basic biology, and the fact that it inhabits an endangered ecosystem (Janzen 1988, Lerdaud et al. 1991) made the Red-breasted Chat a priority species for study. Here, we report on its phenology and habitat use. We also provide the first complete description of nest and eggs, and some details on nesting biology.

METHODS

We conducted our study at the Chamela Biological Station (3,300 ha), which is part of the Chamela-Cuixmala Biosphere Reserve (hereafter, the Reserve), Jalisco, Mexico (19° 22' to 19° 35' N and 104° 56' to 105° 03' W). Weather there is strongly seasonal with distinct rainy (June to October) and dry seasons. The Reserve (13,300 ha) is covered predominantly by undisturbed deciduous forest on dry hillsides, with patches of semi-deciduous forest extending along arroyo floodplains (Lott et al. 1987). Within the Reserve, 24 bird species endemic to Mexico have been recorded; of those, 20 are endemic to western Mexico (Arizmendi et al. 1990). See Vega Rivera et al. (2003) for a detailed description of the study area.

From March 1999 to August 2000, we conducted monthly mist netting along four 3-km-long trails, separated from each other by 1 km. The dominant vegetation types were decidu-

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ous ($n = 2$) and semi-deciduous ($n = 2$) forest. Every month for 3 consecutive days and 5 hr/day, we placed 12 mist nets (12 m \times 2.5 m, 6-mm mesh) along each trail; nets were separated by 100 m. Each chat we captured was banded with numbered aluminum bands and processed for body mass (to 0.1 g with a 50 g Pesola spring scale), bill and tarsus lengths (to 0.05 mm using dial calipers), and length of unflattened wing chord (to 0.5 mm using a flat-ended 15-cm ruler). We determined whether chats were in breeding condition by evaluating the presence of cloacal protuberance or brood patch. Age was evaluated by plumage and, for hatch-year birds, by the presence of unpneumatized areas in the skull.

From May to August 2001, we walked along trails looking for singing males. Once we identified a male's territory, we searched intensively for the nest. Nest-building, food-delivery, and alarm behaviors were used to help us locate nests. Nests were visited every 3 days until clutch completion; nests with complete clutches were visited every day until hatching. We measured and weighed chicks 2 days after the last chick had hatched. Nests were measured after fledging.

We assessed habitat use (deciduous versus semi-deciduous forest; dry versus rainy seasons) and quality by examining chat abundance, age ratio, yearly persistence, and body mass corrected for wing length. Yearly persistence was calculated as the proportion of chats marked during the breeding season (June to September) that were recaptured in the study site during the dry months of January to April.

We used nonparametric Mann-Whitney U -tests (MINITAB, Inc. 1996) to compare captures between seasons and to determine gender differences in mass and wing chord. We tested the null hypothesis of mutual independence among variables (forest type \times season \times gender) by a chi-square three-way test of independence. Since the hypothesis was not rejected, we did not test for partial independence (Zar 1996:507). Statistical significance was set at $\alpha \leq 0.1$. All values are reported as mean \pm SD.

RESULTS

Phenology.—We captured 116 chats (first captures only) during the 18-month period of

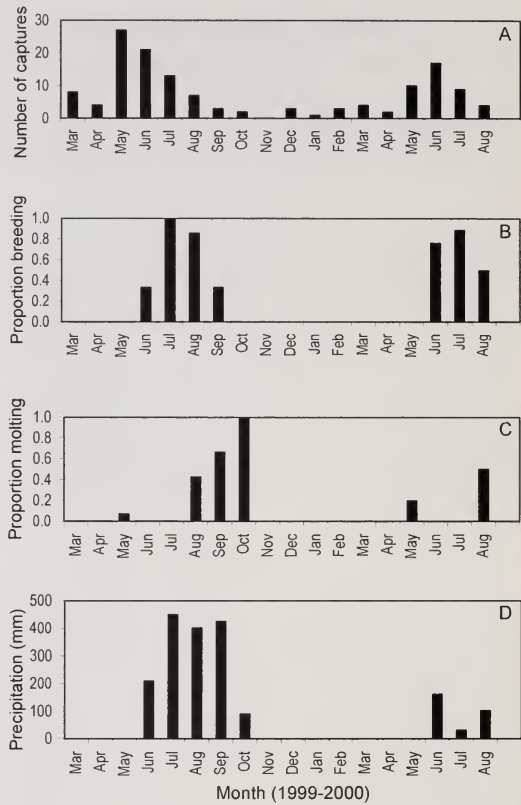


FIG. 1. Monthly distribution of captures of adult Red-breasted Chats (A), proportion of birds in breeding condition (B), proportion of birds molting (C), and precipitation (D) in the Chamela-Cuixmala Biosphere Reserve, Jalisco, Mexico, 1999–2000.

mist netting. Of those, 21 were hatch-year (HY) birds and 95 were after-hatch-year birds (54 males and 41 females). Monthly captures (including recaptures) differed between seasons (Fig. 1A). From May to September (breeding season), the average number of captures per month was 14.0 ± 10.0 , whereas during the rest of the year (non-breeding season) it was 3.0 ± 2.6 (Mann-Whitney U -test, $U = 46$, $P = 0.034$). Chats in breeding condition were captured from June through September ($n = 50$), with the proportion of birds in breeding condition peaking in July (Fig. 1B). Females tended to move longer distances between yearly recaptures (300 ± 386 m) than males (115 ± 109 m; $U = 860$, $df = 54$, $P = 0.092$). Eight males and five females captured during the 1999 nesting season were recaptured in the same nets the following nesting

season (2000). All birds captured from December through February ($n = 8$) were HY and second-year males, and all HY birds ($n = 21$) were captured September–December.

Based on 13 adult chats captured during molt, a complete prebasic molt occurred from August to October. Seven molting HY birds were captured in September and October (Fig. 1C); from four individuals recaptured after their second prebasic molt, we confirmed that immatures attain adult plumage by the second prebasic molt. In May, we captured four chats with light molt on the neck and head.

Habitat use.—Significantly more individuals were captured in the deciduous forest ($n = 88$) than the semi-deciduous forest ($n = 28$) and there were no interactions among forest type, season, and gender ($\chi^2 = 8.04$, $df = 4$, $P > 0.10$). Yearly persistence was lower in the deciduous (0.11) than in the semi-deciduous forest (0.14), but small sample sizes during the dry months (seven and three, respectively) precluded us from conducting a statistically meaningful analysis. No differences occurred in corrected body mass for individuals captured in deciduous (0.21 ± 0.002) versus semi-deciduous forests (0.20 ± 0.003 ; $U = 6,469$, $P = 0.63$). Corrected body mass was lower during the dry season (0.20 ± 0.001) than in the rainy season (0.22 ± 0.002 ; $U = 3,353$, $P < 0.01$).

Nesting biology.—We found 10 nests in July, in both deciduous ($n = 8$) and semi-deciduous ($n = 2$) forest. Nests were attached to a horizontal fork formed by two or three twigs (4.3 ± 0.2 mm diameter) in saplings 141 ± 26 cm high (range: 82–175 cm) and 16 ± 1.3 mm dbh of Euphorbiaceae (*Croton piramidalis*), Myrsinaceae (*Ardisia* spp.), Rubiaceae (*Randia* spp.), Acanthaceae, and Cappareceae. Mean nest height above the ground was 73 ± 19 cm (range: 48–103 cm).

The cup-shaped nests had very thin walls; eggs were visible through some areas of the walls. Primary materials used in nest construction were Spanish moss (*Tillandsia* spp.), thin (<1 mm) tendrils of Cucurbitaceae, inflorescences of *Lassiasis* spp., thin dark fibers, and spider silk; nests were lined with the finer materials. Fiber-like epiphytes (Spanish moss) hung 20–30 cm below the main nest cup, obscuring nest outlines and making nests quite cryptic. Mean nest depth was 4.7 ± 0.3 cm

TABLE 1. Morphological measurements (mm) and mass (g) of 10-day-old Red-breasted Chat nestlings ($n = 6$) and adults ($n = 85$) in the Chamela-Cuixmala Biosphere Reserve, Jalisco, Mexico, 1999–2000.

	Nestlings	Adults ^a
Mass	9.1 ± 0.7	12.1 ± 1.0
Wing chord	34.1 ± 2.4	57.1 ± 2.3
Tarsus	18.5 ± 0.8	19.8 ± 0.6
Culmen	4.2 ± 0.4	12.3 ± 1.9

^a Red-breasted Chats showed significant gender differences in mass (male: 12.17 ± 0.82 ; female: 11.75 ± 0.90 ; Mann-Whitney test, $U = 3,021$, $df = 56, 72$, $P < 0.014$) and wing chord (male: 58.30 ± 1.89 ; female: 55.42 ± 1.75 ; $U = 2,156$, $df = 56, 72$, $P < 0.01$).

and mean inner rim diameter was 5.2 ± 0.9 cm.

We found one nest before egg laying, six during incubation, one with nestlings, and two with pieces of eggshell. Eggs averaged 18.6 ± 0.2 mm (range: 17–20 mm) by 14.3 ± 0.2 (range: 13–17 mm); eggs were white with smooth surfaces. Only females were observed incubating; males spent most of the time singing nearby. Both females and males were extremely wary and typically they departed when we approached the nest. Based on the nest found before egg laying, chats laid one egg per day until clutch completion (four eggs); the incubation period lasted 14 days.

Just-hatched chicks were without feathers and had their eyes closed. At 3 days of age, nestlings had visible pinfeathers on their dorsal and ventral tracts; rectrices and remiges barely protruded at this stage. At 10 days, feathers in all regions were breaking sheaths; rectrices and remiges were almost entirely in sheaths. Primaries and secondaries were brown-gray, and primary and secondary coverts were gray with pale-brown margins (see Table 1 for measurements and weights).

Both males and females fed nestlings; during the first few days of brooding, males presented food to females, who then fed the young. Young fledged at 8–10 days of age, but this may be an underestimate of fledging age due to our activities at nests. Of seven nests found with eggs and one with nestlings, young fledged from only two; three nests with eggs and three with young were depredated.

DISCUSSION

Survey data suggest that Red-breasted Chats are uncommon along the Pacific slope

(Schaldach 1963) and in our study area (Hutto et al. 1985; Hutto 1989, 1994; Ornelas et al. 1993). According to our data, chats are permanent residents in the Chamela-Cuixmala Biosphere Reserve, where they were very common during the breeding season and uncommon the rest of the year. We do not know whether our data reveal real changes in the abundance of this species, or reflect the greater effort of this study. Nevertheless, it is puzzling that far fewer birds were captured during part of the dry season. This pattern suggests either that the birds may become less susceptible to trapping, or that at least part of the population may migrate locally to higher elevations (American Ornithologists' Union 1983) or habitats not sampled during this study (e.g., second-growth forest). Ornelas et al. (1993) suggested that the low detectability of this and other species in Chamela was either because they were rare or because they preferred more humid habitats. However, as we showed earlier, this species was neither uncommon, nor did it seem to prefer the more humid, semi-deciduous habitats. Low numbers recorded for this species could be due to its preference for second-growth habitats during the dry season. However, Hutto (1989, 1994) did not find chats in his study sites outside the Reserve; he reported chats occurring only in the "undisturbed" forest of the Reserve. It is evident that long-term studies are necessary to understand the spatial and temporal distribution of birds historically regarded as sedentary (Winker et al. 1997).

For the chat and other passerines, the end of the dry season seems to mark the beginning of the breeding season (Ornelas et al. 1993; JHVR unpubl. data). Although the first chats in breeding condition were captured in June, other activities such as territory selection and settlement, mate selection by females, nest-site selection, and construction of the nest, may have been initiated earlier. The Yellow-green Vireo (*Vireo flavoviridis*), a species that migrates from South America to breed in the Reserve, shows the same pattern; it arrives in the Reserve in May, but the first birds in breeding condition appear in June (JHVR unpubl. data). In Chamela, insect production starts after the first rains (Lister and Garcia 1992), which in the years of our study occurred in late June (Fig. 1D).

Nests of the Red-breasted Chat resemble those described for the insular subspecies, *G. v. francescae* (Grant 1964), and the Gray-throated Chat (Salgado-Ortiz et al. 2001). Nest dimensions and location are similar, but neither Grant (1964) nor Salgado-Ortiz et al. (2001) mentioned material hanging from the cup. Salgado-Ortiz et al. (2001) reported that only females build the nest and incubate eggs; they also indicated that a complete clutch contains two eggs, whereas most of our nests had four eggs. We believe that this difference may not be real, because they found only one nest with a complete clutch.

Worldwide, tropical deciduous forest may be the most endangered major tropical ecosystem (Janzen 1988). In Mexico, only 27% of the original cover of tropical deciduous forest remained in 1990, and less than 10% of the area covered with deciduous forest is now under some type of protection (Trejo and Dirzo 2000). Stotz et al. (1996) stated that severe habitat disturbance in most dry-forest zones in the Neotropics has greatly affected birds that are deciduous-forest specialists. They identified the Red-breasted Chat as one of eight "indicator" species for conserving tropical deciduous forest of the Pacific lowlands in Mexico. Currently, this forest type is only protected in the Chamela-Cuixmala Biosphere Reserve. We hope the information we provide here will aid in conservation efforts for this species and its habitat.

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Short Communications

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Intraspecific Brood Parasitism in the Northern Flicker

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ABSTRACT.—Although intraspecific brood parasitism is common in many bird species, including several secondary cavity-nesting birds, it does not appear to have been reported in woodpeckers. We report a case of intraspecific brood parasitism in the Northern Flicker (*Colaptes auratus*) in which six to eight eggs were dumped into the host nest box during a 2- to 3-week period. We estimate that the host female laid a clutch of 8 to 10 eggs, and at the end of the nestling period we confirmed that 16 flicker eggs had been laid in the nest box. This instance of egg-dumping by a floater female or another resident female in the same territory or on an adjacent territory, could have been facilitated by a lack of suitable nest sites in the area coupled with intense nest-site competition from European Starlings (*Sturnus vulgaris*). Received 16 October 2003, accepted 24 March 2004.

Intraspecific brood parasitism occurs in a wide variety of bird species (Yom-Tov 1980, Petrie and Moller 1991, Zink 2000, Andersson and Aehring 2001), and has been documented in several secondary cavity-nesting species including European Starlings (*Sturnus vulgaris*; Romagnano et al. 1990, Pinxten et al. 1993, Sandell and Diemer 1999), House Wrens (*Troglodytes aedon*; Picman and Belles-Isles 1988), Tree Swallows (*Tachycineta bicolor*; Lombardo 1988), Eastern Bluebirds (*Sialia sialis*; Meek et al. 1994), Wood Ducks (*Aix sponsa*; Semel and Sherman 2001), and Common Goldeneyes (*Bucephala clangula*; Pöysä 1999). However, documentation of intraspecific brood parasitism (e.g., egg-dumping by a conspecific) in primary cavity-nesting birds such as woodpeckers appears to be absent from the literature. Wiebe (2002) reported an instance of classical polyandry in the Northern Flicker (*Colaptes auratus*) in which a female attended two nests concomitantly, but there was no evidence of brood parasitism. In-

traspecific egg-dumping in cavity-nesting birds, including primary cavity nesters such as flickers, may be common since suitable nest sites are often in short supply (see Brown 1984, Raphael and White 1984, Emlen and Wrege 1986, Picman and Belles-Isles 1988, Li and Martin 1991). Here, we report an apparent instance of intraspecific brood parasitism in a primary cavity-nesting species, the Northern Flicker. Since the flicker pair in question was not color banded, and because we did not conduct a genetic parentage analysis, we cannot be absolutely certain that egg dumping occurred. There is a remote possibility that the paired female may have laid more than one egg per day, although this has never been reported before in any woodpecker species (see Moore 1995).

All observations and nest checks in this study were made by ARB. He observed a pair of nesting Northern Flickers at a nest box in his back yard in Britton, Lenawee County, Michigan, from 8 May to 4 July 2003. The nest box was erected on a pole at a height of 4.4 m, angled slightly downward (for box dimensions see Bower 1994), and was situated in a semi-open area about 35 m from the back door of his residence. Flickers are considered weak excavators (Harestad and Keisker 1989, Winkler et al. 1995), and sometimes use wooden boxes for nesting (Bent 1964, Bower 1995, Ingold 1998). Since European Starlings frequently compete with flickers for nest cavities and boxes (Kerpez and Smith 1990, Ingold 1998), a nest box with a smaller entrance opening (5 cm diameter) designed to live-trap starlings was placed on a pole at the same height, 5 m away. This box was erected to lure starlings away from the neighboring flicker box. To further discourage starlings and attract flickers, the flicker nest box was completely filled with pine woodchips, thus preventing starling entry and allowing the flickers to “excavate” a cavity in the box.

On 8 May, a pair of Northern Flickers be-

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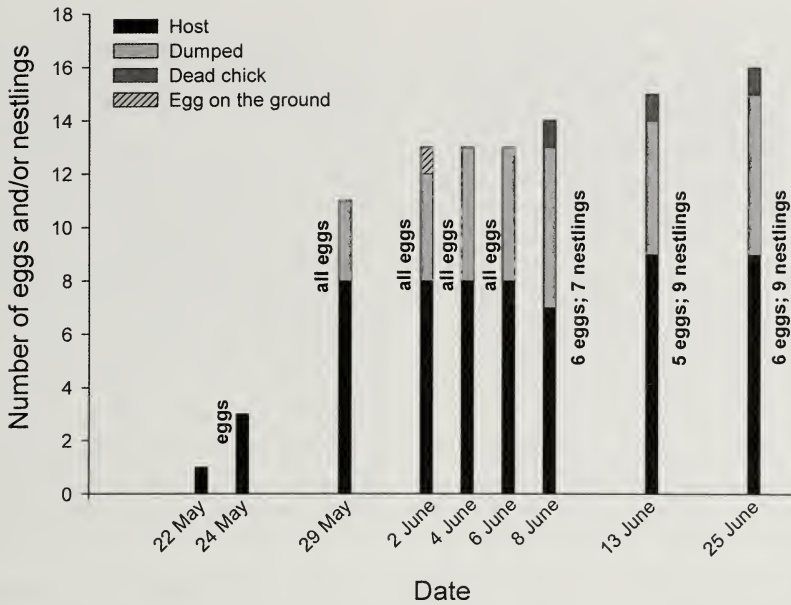


FIG. 1. Nesting chronology of a Northern Flicker pair in Lenawee County, Michigan, 2003, in which intraspecific brood parasitism occurred during a period of 2.5 weeks. Total number of eggs and nestlings found in the nest box on a given day are indicated next to bars. Because it was unclear on 8, 13, and 25 June what proportion of the eggs and nestlings were attributable to the host versus the parasite, we did not attempt to indicate this on the graph. It was also unclear whether the dead chick resulted from an egg that was dumped or laid by the host.

gan excavating woodchips from the flicker box; they had taken up residency in the box by 11 May, although egg-laying had not begun. Between 11 and 15 May, the flicker pair was evicted twice by starlings, in spite of the starling box trap located nearby. After each eviction, the flicker box was repacked with pine chips to discourage the starlings and encourage the flickers to excavate again. By 22 May, a flicker pair had taken up residency in the nest box again, although the contents of the box were not examined on this day. On the afternoon of 24 May, three flicker eggs were found in the box, suggesting that egg-laying was initiated on 22 May. On 29 May, 8 days after the initiation of egg-laying, 11 eggs were found in the nest box (Fig. 1). Although clutch sizes can range from 3 to 13 eggs (see Moore and Koenig 1986, Winkler et al. 1995, Wiebe 2003), female flickers lay only one egg per day (Sherman 1910, Moore 1995); thus a second female flicker dumped at least two and probably three eggs in the nest box between 24 and 29 May (Fig. 1).

ARB first observed apparent incubation be-

havior (continuous sitting) by both a male and female flicker on 29 May. This was probably the original mated pair, although we cannot be sure since the birds were not marked. On 2 June, 12 days after the onset of egg-laying, 12 eggs were found in the box and a single broken egg was found on the ground beneath the box, possibly having been removed by the host pair (removal was not documented). Since the birds initiated incubation about 5 days earlier, it is possible that a second female flicker dumped an additional egg (the egg on the ground) or two (the one in the box) between 29 May and 2 June. However, since flicker incubation typically begins with the penultimate egg (second-to-last; K. L. Wiebe pers. comm.), we assigned one of the two eggs to the resident female (egg laid on 30 May), and assumed that the other was dumped between 30 May and 2 June. Thirteen flicker eggs were found in the box on both 4 and 6 June, well after the onset of incubation, indicating that another egg had been dumped in the host box (Fig. 1). On 8 June, seven 1-day-old flicker nestlings, six unhatched eggs and

a single dead nestling were found in the box. This indicates that by 7 or 8 June, an additional egg was dumped into the host box since only 13 eggs were present on 6 June (Fig. 1). On 13 June, there were nine nestlings about 6 days old and five unhatched eggs (which were then removed). Since a single dead nestling had been removed on 8 June, our findings of 13 June suggest that an additional egg had been dumped into the box between 8 and 13 June (nine nestlings, five eggs, and one nestling that died; Fig. 1). By this point, 15 eggs had been laid in the host box, 8 or 9 of which were likely laid by the host female. The contents of the box were checked on several occasions between 13 and 24 June and on each occasion all nine nestlings were present. On 25 June, a large number of mites were found in the nest box; subsequently, the nestlings were removed and placed in a new box on the same pole. Upon examining the remaining nest contents of the original box, one additional flicker egg was found buried in the woodchips. Thus, a total of 16 eggs had been laid in the nest box during this reproductive effort with at least 6 and perhaps as many as 7 or 8 eggs having been dumped by at least one additional female. Between 26 June and 4 July all nine nestlings fledged.

Additional evidence suggesting that an extra-pair flicker may have dumped eggs into the resident flicker pair's nest box occurred on 9 June, when a female flicker landed on the roof of the nest box. This individual put on a conspicuous display by fanning her tail feathers and raising the feathers on the top of her head. When she peered into the nest box, the male that was in the box brooding the nestlings exited and aggressively chased this female to a nearby tree and then further pursued her more than 40 m from the box. About 1 hr later a female returned to the box and was again chased from the area by the resident male.

Intraspecific brood parasitism in Northern Flickers has not been reported previously. As in any cavity-nesting species, it is possibly the result of a shortage of suitable nest sites (Yom-Tov 1980, Picman and Belles-Isles 1988, Sandell and Diemer 1999) and/or the loss of a nest cavity during the egg-laying or incubation period (Yom-Tov 1980). Ingold (1998) found that European Starlings prefer to usurp freshly excavated flicker nest cavities

rather than use nearby, vacant nest boxes. In such instances, the benefits of intraspecific egg dumping might outweigh the costs of excavating a new cavity (assuming a suitable nest site is available) and starting the nesting cycle over. Wiebe (2003) developed a model that demonstrates that even in the face of intense starling competition, it virtually always benefits flickers to nest early rather than delay reproduction, except when the risk of cavity usurpation by starlings is very high (~75%). In any case, egg-dumping should be a profitable strategy for the brood parasite because its young are reared at no cost. The results of this study, in which the resident female laid a clutch of 8 or 9 eggs, and ultimately hatched 10 chicks, provide some evidence that intraspecific brood parasitism may be profitable.

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Common Loon Pairs Rear Four-Chick Broods

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ABSTRACT.—Common Loons (*Gavia immer*) normally lay a single clutch of two eggs each breeding season. They occasionally lay one- or three-egg clutches, and rarely, four-egg clutches. Participants of the Canadian Lakes Loon Survey provided seven independent observations of loon pairs rearing four-chick broods. Photographic evidence confirmed two separate instances of adult loon pairs at Anglin Lake, Saskatchewan, and Kashaabog Lake, Ontario, exhibiting parental behavior toward a four-chick brood. Occurrence of four-chick broods may be the result of supernumerary clutches, nest parasitism, post-hatch brood amalgam-

ation, or a combination of these factors. *Received 8 July 2003, accepted 24 March 2004.*

Supernumerary broods, either as a result of nest parasitism by unrelated conspecifics, supernumerary clutches, or post-hatch brood amalgamation, are relatively common among grebes (Storer and Nuechterlein 1992, Cullen et al. 1999, Muller and Storer 1999, Stout and Nuechterlein 1999, Stedman 2000) and waterfowl (Afton and Paulus 1992:90, table 3–21; Sayler 1992). However, there are few documented instances of supernumerary broods in loons (Barr et al. 2000), including the most widely studied species, the Common Loon

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(*Gavia immer*; McIntyre 1988:30, McNicholl 1993).

Common Loons are large, long-lived waterbirds that normally lay a single clutch of two eggs each breeding season, although occasionally they will lay one or, even less frequently, three-egg clutches (Peck and James 1983, Croskery 1991, McIntyre and Barr 1997). The frequency of three-egg clutches reported for Common Loons is low and ranges from 0.5% (Campbell et al. 1990) to 0.8% (Peck and James 1983, McIntyre 1988:table 2–5). Clutches containing four eggs are rare, but have been noted several times (Nelson 1983, Peck and James 1983, Zicus et al. 1983, McNicholl 1993). To our knowledge, there is no confirmed record of Common Loons rearing four-chick broods. In this paper we report seven instances of Common Loon adults accompanying and rearing four-chick broods, two of these confirmed by photographic records.

METHODS

Data were gathered by volunteer participants of the Canadian Lakes Loon Survey (CLLS), who monitored Common Loon breeding pairs on lakes, rivers, and bays throughout Canada. Participants selected their own water body or portion of a water body to survey breeding loons and recorded observations of breeding pairs at least once during each of three time periods: nesting (early June to mid-July), hatching and early brooding (early to late July), and pre-fledging (mid-August to mid-September). All surveys lasted a minimum of 2 hr and often were supplemented by incidental observations. During each survey, observers recorded the date, survey method (e.g., from a single point on shore, walking along shoreline, or from a boat or canoe), maximum number of adult loons observed (including paired loons), maximum number of mated loon pairs present, and maximum number and age class of young. The CLLS survey protocol instructed volunteers to classify chicks as downy young (<1/3 adult

length with dark gray down feathers), small young (1/3 to 2/3 adult length with light brown-gray or mottled-gray down feathers) or large young (2/3 adult length or longer with a full coat of light and dark gray feathers). Although not part of the survey protocol, CLLS participants often found loon nests during surveys and recorded clutch sizes. Periodically, participants also provided photographic records of observations during surveys. These records provided the basis for results reported here.

RESULTS AND DISCUSSION

Since the initiation of the CLLS in 1981, participants have reported 6 of 687 (0.87%) loon nests containing three-egg clutches and no four-egg clutches. CLLS participants reported 45 of 6021 (0.75%) Common Loon pairs with supernumerary broods (>2 chicks), which is similar to values that others have reported for this species (see above). In five separate instances, CLLS participants provided written evidence of four-chick Common Loon broods: two on Shepherd Lake, Ontario (44° 39' N, 81° 7' W) during 1983 and 1984; one on Oak Lake, Ontario (44° 36' N, 77° 55' W) during 1984; and two on the Mactaquac River, New Brunswick (46° 01' N, 66° 58' W) during 1988 and 1993. Participants also provided photographic evidence of two separate instances of Common Loon pairs accompanied by four-chick broods. The first photograph was taken on 14 July 1999 at Anglin Lake, Saskatchewan (53° 44' N, 105° 56' W; Fig. 1A). This group of birds was observed intermittently from 14 July to 17 August 1999. CLLS participants estimated these chicks to be 3 weeks of age on 14 July, and adults exhibited feeding behavior toward all four chicks.

Photographic evidence was also secured at Kashaabog Lake, Ontario (44° 38' N, 77° 57' W; Fig. 1B, C), where a Common Loon pair was observed attending four chicks from 21 July to 30 September 2001. CLLS participants estimated this four-chick brood to be 3 weeks

FIG. 1. Photographs of two different pairs of adult Common Loons with four-chick broods: (A) Anglin Lake, Saskatchewan, Canada, 14 July 1999 (photograph by W. R. and E. V. Hoffman), and (B and C) Kashaabog Lake, Ontario, Canada, July 2001 and August 2001, respectively (photographs by P. Grisson).

A



B



C



of age on 21 July, and adults exhibited feeding behavior toward all four chicks. Observations later that summer showed that one of these chicks was smaller than the other three, and often it was observed farther away from the adults than the other chicks (Fig. 1C).

Occurrence of four-chick broods in Common Loons may be the result of supernumerary clutches, nest parasitism, post-hatch brood amalgamation, or a combination of these factors (Nelson 1983, Zicus et al. 1983, Belant and Olson 1991, McNicholl 1993). Both Nelson (1983) and Zicus et al. (1983) discounted the occurrence of four-egg clutches as a result of nest parasitism, suggesting that nest parasitism was unlikely due to aggressive territory defense exhibited by breeding loons. Four-egg clutches have been documented twice for Red-throated Loons (*Gavia stellata*); in both instances two different females were observed laying eggs in the same nest (Barr et al. 2000). Supernumerary clutches have been documented several times for Common Loons (see McNicholl 1993). However, there are only two confirmed reports of supernumerary clutches hatching successfully in Common Loons; McIntyre (1988) found two three-egg clutch nests on two different lakes, and later observed a brood of three young on each of these same lakes.

Adult loons may adopt chicks if the young become separated from their natal parents due to inclement weather (Strong and Bissonette 1989), human disturbance (Robertson and Flood 1980, Clay and Clay 1997), or parental abandonment (Gingras and Paszkowski 1999). Persistent wind and wave action can separate loon chicks from their natal parents (Sjolander and Agren 1976). On Anglin Lake in 1999, poor weather conditions occurred from 30 June through 6 July, and a severe hailstorm occurred on 12 July (W. R. Hoffman and E. V. Hoffman pers. comm.). Thus, weather conditions existed that could have resulted in chicks becoming separated from their natal parents and then being adopted by one of several other breeding pairs on Anglin Lake.

Post-hatch brood amalgamation can also occur when brood densities in breeding areas are high (Afton and Paulus 1992). Anglin Lake (1,500 ha) consistently had the highest annual number of breeding loon pairs recorded (mean of 38 pairs/year from 1996 to 2002)

on a lake by the CLLS. Concentrations of loon pairs on Anglin Lake were high on 14 July 1999, when 36 separate Common Loon pairs were observed. Size and behavioral differences in the brood photographed at Kasshabog Lake also suggested brood amalgamation. Intensive monitoring and/or genetic evidence are required to determine definitively whether supernumerary broods in Common Loons result from supernumerary clutches, nest parasitism, or post-hatch brood amalgamation.

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A Possible Foraging Association between White Hawks and White-nosed Coatis

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ABSTRACT.—Some species of birds commonly forage by following other animals and capturing prey flushed by the movements of the latter. Here we describe a possible foraging association between White Hawks (*Leucopternis albicollis*) and white-nosed coatis (*Nasua narica*) in Tikal National Park, Guatemala. The frequency of association varied seasonally, perhaps due to differences in availability of reptiles, the hawks' main prey. Received 28 January 2003, accepted 26 March 2004.

Many species of birds habitually forage by capturing prey flushed by other animals. For instance, Barred Forest-Falcons (*Micrastur ruficollis*) frequently follow army ants (Willis

et al. 1983, Thiollay and Jullien 1998), and Double-toothed Kites (*Harpagus bidentatus*) associate with several species of primates (e.g., Fontaine 1980, Egler 1991). There are occasional reports of other Eastern and Western hemisphere raptors that appear to forage in association with a variety of mammalian carnivores, although prey capture has been observed only rarely (e.g., Sliwa 1994, Silveira et al. 1997).

Here, we describe a possible association between White Hawks (*Leucopternis albicollis*) and an omnivorous mammal, the white-nosed coati (*Nasua narica*), in the lowland tropical forest of Tikal National Park, Guatemala. White Hawks, which prey primarily on snakes and lizards (Draheim et al. in press), have been documented following monkeys in Costa Rica (Boinski and Scott 1988) and French Guiana (Thiollay and Jullien 1998, Zhang and Wang 2000). White-nosed coatis are diurnal procyonids; their diet consists primarily of

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leaf litter-dwelling invertebrates and fruit (Kaufmann 1962, Russell 1982). They are predominantly terrestrial during active periods, but they rest and sometimes forage in trees. In Tikal, females and juveniles live in very large bands; one of our study bands contained 162 animals (Booth-Binczik 2001).

We studied coatis in Tikal (17° 13' N, 89° 37' W; elevation: 130–400 m) from June 1994 to November 1996. The mean annual temperature is approximately 26° C, with the lowest monthly mean occurring in January and the highest in May. There is a pronounced dry season from January through April, and many trees lose their leaves in March and April.

We observed White Hawks opportunistically while we studied marked, habituated bands of coatis. The bands were so large that typically we could see only a small percentage of band members at one time. Because we watched coatis mainly on the ground and could not see an entire band at once, we probably overlooked some accompanying hawks. During a 22-month period, we located coati bands 458 times and observed White Hawks with the bands on 52 (11%) of those occasions. White Hawks were observed with coati bands throughout the year, but more frequently during January and February (frequency of association = 24%) than during other months (8%). We saw White Hawks with six different coati bands throughout an area of about 14 km², equal in size to the nesting territories of 3–4 pairs of hawks (Draheim et al. in press).

Most of the time that hawks were in view they were perched in the lower portion of the canopy directly above the coatis. They kept pace with foraging bands by flying from tree to tree as the coatis moved along. On at least three occasions we observed a hawk following a band for 2–3 hr. On occasion there were two hawks with a band at the same time. The coatis never displayed any alarm at the presence or movement of the hawks, and the hawks were never seen directing any movements toward coatis. We saw no predation attempts by White Hawks accompanying coatis.

Although we did not observe prey capture, it is possible that the hawks were following coati bands for the purpose of preying upon animals that were flushed by the coatis, as in other foraging associations. As coatis forage along the forest floor, they rummage through

the leaf litter with their noses, dig into the soil, turn over small objects, and tear apart pieces of rotten wood. Coatis may be particularly useful to White Hawks in that they frequently display direct alarm displays toward some species of snakes and lizards (GAB unpubl. data), possibly indicating to a hawk the presence and location of possible prey items. In the foraging associations of many species, insects are the primary prey consumed by birds, but there is evidence that reptiles also can be located in this manner. During a 2-year study of brown capuchins (*Cebus apella*) in French Guiana, White Hawks were present during 11% of the monkeys' active time, and they were observed capturing arboreal snakes seven times while accompanying the monkeys (Zhang and Wang 2000). Double-toothed Kites have been observed catching lizards flushed by monkeys (Fontaine 1980, Boinski and Scott 1988). Many bird species that associate with army ants have been seen preying on lizards (Mays 1985, Coates-Estrada and Estrada 1989), and in Tikal we saw a Roadside Hawk (*Buteo magnirostris*) capture a snake that was fleeing a swarm of army ants (SDBB unpubl. data).

Although the seasonal peak in association between White Hawks and coatis could be due to a peak in hawk density (seasonal patterns of which are unknown in Tikal), it is more likely related to the hawks' reliance on reptilian prey. January and February are the coldest months of the year in Tikal; thus, reptiles would be least active and most difficult to find at that time. Studies in Costa Rica (Boinski and Scott 1988) and Brazil (Rodrigues et al. 1994) revealed that several species of insectivorous birds associated with monkeys most often during seasons when insects were least abundant. Researchers who have observed coati bands in other locations (e.g., Panama, Costa Rica) have not reported foraging associations with White Hawks or any other birds. It may be that White Hawks associate with coatis only in relatively temperate areas where the diversity of primate species is low. The relationship between White Hawks and coatis deserves further investigation to ascertain whether the hawks obtain significant amounts of prey through this association.

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First Breeding Record of Wilson's Plover (*Charadrius wilsonia*) from the Pacific Coast of Colombia

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ABSTRACT.—Wilson's Plover (*Charadrius wilsonia*) occurs year-round along the Caribbean and Pacific coasts of Colombia. The species frequents a variety of coastal habitats including sandy beaches, tidal flats, and small swamps and wetlands. Its breeding range extends from Virginia south through the West Indies to Surinam, and from Baja California to Peru. Here, we report the first nesting record on the Pacific coast of Colombia. Received 14 June 2003, accepted 10 March 2004.

All three sub-species of Wilson's Plover (*Charadrius wilsonia wilsonia*, *C. w. beldingi*, and *C. w. cinnamominus*) have been recorded in Colombia. The first records (*C. w. wilsonia* and *C. w. cinnamominus*) came from Colombia's Caribbean coast. These observations included breeding displays, but no nests were found (Naranjo 1979). On the Pacific coast, Wilson's Plovers (*C. w. wilsonia* and *C. w. beldingi*) were first reported during a study of chronological distribution and habitat selection of shorebirds at Buenaventura Bay (Naranjo et al. 1987). Although population estimates of resident Wilson's Plovers along Colombia's Pacific coast have ranged into the hundreds (Franke 1986, Naranjo et al. 1987, Aparicio et al. 1996, Naranjo and Mauna 1996) and the species has been considered a coastal breeder from Baja California to Peru (Johnsgard 1981, Hayman et al. 1986, Canevari et al. 2001), there are no breeding records

for Colombia's Pacific coast (Hilty and Brown 1986, Salaman et al. 2001).

On 13 May 1993, we participated in a shorebird survey of Punta Soldado Island, Buenaventura Bay (03° 49' 55" N, 77° 08' 40" W), conducted by the Association for the Study and Conservation of Aquatic Birds in Colombia (CALIDRIS). Punta Soldado beaches are essentially unaffected by tides (possibly flooded once per year), are sparsely vegetated, and serve as roosting and foraging sites for numerous migratory shorebirds and terns (Aparicio et al. 1996, Naranjo and Mauna 1996). We observed two *C. wilsonia* adults (male and female) exhibiting defensive behaviors in the berm zone of the beach. From a distance of approximately 20 m, we observed the male plover perform *head-up* displays accompanied by *tweet* calls while the female plover adopted a *squatting* posture. Subsequently, we observed three Wilson's Plover chicks 0.5 m from the female. As we approached more closely, the male responded with a short *crouch-run* and the female responded with a stationary *broken-wing* display accompanied by a buzzy *distraction* call (see Bergstrom 1988 for description of alarm and distraction displays). These observations confirm breeding of Wilson's Plovers on the Pacific coast of Colombia.

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First Description of the Nest, Eggs, Young, and Breeding Behavior of the Great Antpitta (*Grallaria excelsa*)

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ABSTRACT.—We provide the first description of the nest, eggs, young, and breeding behavior of the Great Antpitta (*Grallaria excelsa*) in Yacambu National Park, Venezuela. The nests ($n = 3$) were large, bulky, open-cup structures composed of a dense assortment of live and dead mosses, rootlets, wet leaves, small stems, detritus, and live and dead fern fronds, and were lined with a thick mesh of black rootlets and rhizomorphs. Nests were built >3.8 m above the ground in live trees where dense clusters of aroid plants, epiphytes, and lianas secured them to either a vertical fork or against the trunk itself. Both adults participated in nest building; incubating two unmarked, turquoise eggs; and feeding nestlings. Mean nest attentiveness (time spent on the nest/total video time when corrected for human disturbance) was $98.8 \pm 1.8\%$ SD, and nestling feeding rates were low (one visit by each adult/5 hr total video time). Received 10 September 2003, accepted 25 March 2004.

Antpittas (Formicariidae) are a diverse group of terrestrial antbirds inhabiting the Neotropics, yet the breeding biology of many species is unknown due to their secretive habits and preference for dense understory. The Great Antpitta (*Grallaria excelsa*) is a large (218–266 g), rare species endemic to mid-elevation (1,700–2,300 m), wet, humid forests of Venezuela (Gilliard 1939, Ridgely and Tudor 1994, Hilty et al. 2003). While a few aspects of its ecology have been reported (Hilty et al. 2003), its nest and breeding behavior are still unknown. Here, we describe nesting activity and characteristics of three nests found in May and June 2003 in montane, wet, primary forest in Yacambu National Park, Lara State, Venezuela (09° 24' N, 69° 30' W; 1,800–2,000 m elevation).

During the dry months of March and April 2003, we observed *G. excelsa* foraging in canyons, on ridges, and in swampy areas throughout the forest (approximate canopy height = 25 m). Later in the season (May and June), individuals were observed exclusively in close

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proximity to the junctions of ephemeral creeks created during periods of greater precipitation. Often we located adults by their song—a single phrase, repeated at regular intervals (10-sec pauses between phrases), and characterized as a resonant, hollow, *Otus*-like tone that increased in frequency (710–820 Hz; 4–5 sec phrases; 22 notes/sec; all measurements made with Raven software; spectrograms made with a 200-Hz bandwidth and Hann window function). Most birds sang from a fallen tree or perch <4 m in height. More frequently, we located adults as they foraged silently—alone or in pairs—along creeks, on the edges of treefall gaps, and near large, fallen trees. They foraged exclusively on the ground, moving in quick, short starts, and usually hopping on both legs. Numerous times we also observed adults foraging opportunistically at the edge of an antswarm.

All three nests were located approximately 50 m from the junctions of different ephemeral creeks. The first nest was 3.8 m above ground and built against the trunk of a spiny tree-fern (Cyatheaceae; height = 14 m; dbh = 24 cm; located on a 21° slope). The second nest was located 4.8 m above ground in the fork of a *Pseudobombax* spp. (height = 7.9 m). The third nest was 12 m above ground where two thick branches forked from the trunk of a large, unidentified tree (30 m in height). All three nests were supported by dense clusters of aroid plants, epiphytes, and lianas that offered considerable concealment. Nest, tree, and canopy heights were made using a clinometer.

Nests were large, bulky, open-cup structures with a shallow cup. The first nest had an outside diameter of 40.0 cm, external height of 18.0 cm, cup diameter of 14.0 cm, and a cup depth of 8.0 cm. The second nest had an outside diameter of 35.0 cm, external height of 27.0 cm, cup diameter of 12.0 cm, and a cup depth of 7.0 cm. Nests were composed of a dense amalgamation of live and dead mosses, thin dark-colored rhizomorphs, and dead leaves; pieces of live and dead ferns, palm fronds, and thin sticks were scattered throughout but less numerous. The nest cups were uniformly lined with a tight mesh of thin black and brown rootlets and rhizomorphs that merged with differently colored live and dead mosses on the cup rim.

The first nest was found on 25 May and monitored for 13 days during the incubation period until it was depredated. The nest contained two turquoise, unmarked, slightly glossy, oval-shaped eggs. One egg weighed 17.09 g and measured 38.0 × 30.0 mm. The second weighed 17.64 g and measured 37.4 × 30.0 mm. We videotaped the nest three times during monitoring for 5–8 hr per recording episode (28 May, 10:10–17:40 AST; 30 May, 08:20–16:30; 05 June, 08:00–13:16). Videotapes showed that both the male and female participated in incubation; exchange of incubating parents occurred simultaneously in 2 of 11 instances. Mean on-bout duration was 92.3 ± 41.5 min SD ($n = 12$ on-bouts; range: 36–160 min; 1,207 min total video time; 3 days of filming). Mean nest attentiveness (percent total video time parents were observed incubating) was 91.0 ± 1.0% ($n = 3$ days of filming; 1,207 min total video time; 12 on-bouts). The nest was never left unattended for more than 7 min, except following human disturbance. After correcting for those times when the adult was flushed from the nest during video initiation and tape changes, mean nest attentiveness was 98.8 ± 1.8% ($n = 3$ days of filming; 1,108 min total video time; 12 on-bouts).

Incubation videos revealed that vocal communication around the nest occurred in the form of repeated songs and muted trills, usually just before or following an incubation exchange. Muted trill-songs heard on tape were less common, and it is unclear whether the songs were from the incubating bird or its mate. *G. guatemalensis* has also been reported to sing muted trills from the nest (Dobbs et al. 2003).

The second nest was found on 5 June and monitored during the nestling period until 7 June, when the nest was found empty and undisturbed. On 5 June the nest contained only one nestling and was found on the day before the nestling's primaries emerged from the feather shafts. On that same day and after 1 hr of observation, an adult approached the nest quietly, fed the nestling, and left shortly thereafter. While at the nest, the adult was wary, pausing before, during, and after feeding the nestling to survey the nest area.

Videotapes on 6 June, from 07:00 to 12:00, showed that both parents fed the nestling in-

frequently (one visit each in 5 hr), but delivered large amounts of what appeared to be earthworms (Annelida) and arthropods. One parent brooded the nestling from 07:00 to 07:35, after which time the nestling was left unattended. One adult returned to the nest 1 hr later with food, fed the nestling, and carefully surveyed the nest area before leaving. Its mate arrived 2 sec later, fed the nestling, ate a fecal sac, and then departed. No other visits to the nest were made for the remainder of recording.

On 6 June, the day its primary feathers emerged, the nestling weighed 98 g, lacked tail feathers, and had tarsus and wing chord lengths of 35.80 mm and 50.06 mm, respectively. Its plumage was similar to that of the adults: the breast feathers were scalloped, and its down and emerging tail and wing feathers were light olive-brown. The bill was bright orange, whereas the gape was a striking, bright-red hue.

The third nest was found on 18 June, also in close proximity (<40 m) to a creek junction. This nest was approximately 40 m from the second nest where the nestling had disappeared approximately 11 days earlier, and was likely the re-nest of that same pair. Both adults were observed building the nest. One adult collected nest material while the other sang repeatedly near the base of the nest tree. The pair also brought nesting material to the nest site together, taking turns adding their material while the mate perched close by.

Consistent with observations of other *Grallaria*, both adults of *G. excelsa* participated in nest building, incubation, and feeding nestlings (Wiedenfled 1982, Dobbs et al. 2003, Freile and Renjifo 2003, Price 2003). Mate feeding at the nest was not observed during building, incubation, or the nestling period, but may occur away from the nest as it does in other Formicariidae (Skutch 1969, Dobbs et al. 2003, Price 2003). Also, low rates of nestling feeding have been found in *G. carrikeri* and *G. guatemalensis* (Wiedenfled 1982, Dobbs et al. 2003). Because plumages of males and females are similar, we could not determine gender differences in parental care. Clutch size in *G. excelsa* may range from one to two eggs; it is unclear whether the single nestling of the second nest described above originated from a clutch of one or two eggs.

Other members of *Grallaria* are reported to incubate only one egg (Whitney 1992), or fledge only one young from an initial clutch of two eggs (Dobbs et al. 2003; P. R. Martin pers. comm.).

Egg color and shape were similar to those of all other *Grallaria* described to date (Wiedenfled 1982, Quintela 1987, Whitney 1992, Dobbs et al. 2003, Freile and Renjifo 2003, Price 2003). In addition, nest composition, structure, and placement were similar to those of most other *Grallaria*; however, these traits vary over a species' range and among individuals, as a variety of substrates and building materials have been reported within a single species (Wiedenfled 1982, Quintela 1987, Whitney 1992, Dobbs et al. 2003, Freile and Renjifo 2003, Price 2003). Nests of *G. excelsa* were located in the forest interior, close to the confluence of ephemeral waterways, and were found during the rainy season. Other reports of *Grallaria* nesting habits indicate that all members of the genus may breed during the wet season (Dobbs et al. 2003, Freile and Renjifo 2003).

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Blue-crowned Motmot (*Momotus momota*) Predation on a Long-tongued Bat (*Glossophaginae*)

Eduardo Chacón-Madrigal¹ and Gilbert Barrantes^{1,2}

ABSTRACT.—We report the first record of a Blue-crowned Motmot (*Momotus momota*) feeding on a long-tongued bat (*Glossophaginae*) in a secondary forest in southwestern Costa Rica. The motmot incapacitated the bat, then swallowed it alive, head first. Motmots and bats are found in close proximity along river banks where the former nests and the latter roosts. Received 16 October 2003, accepted 26 March 2004.

Bats are regular food items in the diet of some Neotropical birds (Rodríguez-Duran and Lewis 1985, Lee and Kuo 2001). For example, in the Neotropics some raptors (e.g., Bat Falcon; *Falco rufigularis*) and owls (e.g., Barn Owl; *Tyto alba*) often prey on bats (Table 1), and the Great Potoo (*Nyctibius grandis*) regularly preys on bats on the wing (Boinski and Timm 1985, Fleming 1988, Stiles and Skutch 1989, Braker and Greene 1994). Nevertheless, bat predation is relatively uncommon in the Neotropics. Here, we report the first account of a Blue-crowned Motmot (*Momotus momota*) consuming a long-tongued bat (*Glossophaginae*).

Blue-crowned Motmots consume a large variety of items, including invertebrates (e.g., earthworms, large spiders, mollusks, and insects), fruits, and small vertebrates (e.g., fish, frogs, lizards, snakes, small mammals, small

birds, and nestlings) (Orejuela 1980, Stiles and Skutch 1989, Remsen et al. 1993, Master 1999, Snow 2001). Bats, however, have not been reported as a part of their diet.

At 15:30 hr CST on 12 April 2003, in old secondary forest at Dos Brazos de Río Tigre (08° 31' N, 83° 24' W), Península de Osa (elevation 100 m), Costa Rica, we observed (from a distance of 6 m, using binoculars) a Blue-crowned Motmot feeding on a long-tongued bat. The bat was identified on the basis of its noseleaf, body size, and the long tongue that hung from its partially open mouth. The bat could have been a species of *Glossophaga*, or *Hylonycteris underwoodi*, the two *Glossophaginae* species with characteristics that match those of the individual observed. The former—represented by two species in the Península de Osa—is more common.

When first observed, the motmot was perched on a horizontal branch 1.5 m above the ground, holding the neck of the live bat in its bill. During the next 2–3 min the bird shook the bat up and down violently while grasping it tightly in its bill. It did not strike the bat against the perch as motmots usually do with large larvae and other insects. The motmot then swallowed the bat whole, head first. This behavior suggests that the violent shaking was probably used to immobilize the prey before swallowing it. The motmot remained on the same perch for approximately

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TABLE 1. Costa Rican bird species reported to feed on bats (Boinski and Timm 1985, Fleming 1988, Stiles and Skutch 1989, Braker and Greene 1994, Michalak 1997, Lee and Kuo 2001). Measurements (mean \pm SD) were taken from specimens deposited in the Museo Nacional de Costa Rica and Museo de Zoología, Universidad de Costa Rica.

Common name	Species	Gape (mm)	Weight (g)	n
Double-toothed Kite	<i>Harpagus bidentatus</i>	21.3 \pm 2.0	175.2 \pm 8.5	4
Crane Hawk	<i>Geranospiza caerulescens</i>	22.6	345	1
Sharp-shinned Hawk	<i>Accipiter striatus</i>	17.2 \pm 1.6	na ^a	3
Red-tailed Hawk	<i>Buteo jamaicensis</i>	33.5	800.5	1
Collared Forest-Falcon	<i>Micrastur semitorquatus</i>	24.9 \pm 2.1	772.0 \pm 69.3	2
Bat Falcon	<i>Falco rufigularis</i>	20.9 \pm 1.3	214.6	2
Peregrine Falcon	<i>Falco peregrinus</i>	29.8 \pm 4.7	na ^a	2
Barn Owl	<i>Tyto alba</i>	24.4 \pm 2.1	449.0 \pm 49.9	3
Tropical Screech-Owl	<i>Megascops choliba</i>	18.4 \pm 0.2	163.5 \pm 25.6	3
Spectacled Owl	<i>Pulsatrix perspicillata</i>	38.9 \pm 1.3	765.7 \pm 84.6	3
Mottled Owl	<i>Ciccaba virgata</i>	27.7 \pm 0.1	250.8 \pm 13.2	2
Black-and-white Owl	<i>Ciccaba nigrolineata</i>	30.7 \pm 0.6	336.0 \pm 55.2	2
Great Potoo	<i>Nyctibius grandis</i>	59.6	500.0	1
Blue-crowned Motmot	<i>Momotus momota</i>	21.1 \pm 2.3	114.8 \pm 16.1	6

^a na: data not available from specimens.

30 min after swallowing the bat and then flew away.

In Dos Brazos de Río Tigre, long-tongued bats roost in tree cavities and banks along rivers (LaVal and Rodríguez-H 2002). Because motmots also construct their nests in banks and frequently perch along rivers and streams, it is possible that the motmot captured the bat from a bank roost. The ability to swallow such a large prey item is surprising, considering that the gape width of a Blue-crowned Motmot is relatively small (21.1 mm), compared to the gape of several raptors that prey on bats (Table 1). The Great Potoo, which also feeds on bats, has a much wider gape (59.6 mm). Ingesting the bat by swallowing it whole was quite different from the way small raptors tear pieces from prey items (Thiollay 1994). It is likely that bats make up part of the diet of other bird species; however, predation on bats is probably infrequent, making it difficult to document.

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Ornithological Literature

Edited by Mary Gustafson

BIRDS OF OREGON: A General Reference. Edited by David B. Marshall, Matthew G. Hunter, and Alan L. Contreras. Illustrated by Elva Hamerstrom Paulson. Oregon State University Press, Corvallis, Oregon. 2003: 752 pp., line illustrations. \$65.00 (cloth). This voluminous tome, covering Oregon and its coastal waters, is an excellent reference on the spatial and temporal distribution of birds in Oregon. It is also a rich natural history of birds with useful habitat and foraging descriptions included in most species accounts.

This is an important reference for professionals, students, and birders interested in Oregon's avifauna. Breeding Bird Survey, Christmas Bird Count, and Oregon Breeding Bird Atlas data are compiled, along with anecdotal reports and capture results, to illustrate species distributions. The book covers 486 species recognized by the Oregon Bird Records Committee as having occurred in the state. Atlas-style distribution and abundance maps, derived from the Oregon Breeding Bird Atlas, are presented for 205 Oregon-breeding species. Species nomenclature and sequence follow the 7th edition of AOU's *Check-list of North American Birds* and subsequent check-list supplements. Coverage at the subspecies level is based upon specimens verified by the Taxonomic Editor, M. Ralph Browning.

The editors recognize that their book is the successor to Gabrielson and Jewett's *Birds of Oregon*, published in 1940, and which used data through 1935. The 2003 publication begins with a synopsis of avifaunal change in Oregon since 1935. The first and second chapters, which describe avian habitats in Oregon Ecoregions, document vast changes in land use, avifaunal distribution, and coverage by investigators and birders since 1935 that made this new Oregon avifaunal reference necessary.

Contributions from 100 authors, including many of Oregon's most accomplished and expert ornithologists, make up the body of this reference. Each species account begins with an introductory section that provides a phys-

ical description and any notes of interest. Each account includes a section on *General Distribution, Oregon Distribution, Habitat and Diet, Seasonal Activity and Behavior, Detection, and Population Status and Conservation*. The species accounts are a blend of occurrence and population data (site specific and county locations, dates, population estimates) and anecdotal snippets that are quite readable.

The treatments of extirpated, introduced, escaped, and unaccepted-record species in the Supplemental Species List (Chapter 4) are thorough and provide a satisfying historical perspective. The concise Glossary is very useful in defining or clarifying ornithological and biological jargon without the excessiveness often found in such reference books. A vast list of citations, personal communications, and unpublished reports and data documents the information provided.

A minor criticism of *Birds of Oregon: A General Reference* is the inconsistent presentation, among species accounts, of unpublished data from research and monitoring projects and the reference to museum specimens. Some account authors included many such resources while others included few. Whereas all authors produced excellent accounts, it is disappointing that greater effort was not made to seek out unpublished data. Again, this is a minor criticism and is, perhaps, more appropriately directed toward those who have not published their results!

Overall, the book's illustrations are accurate and a pleasure to view. The line drawings of birds that embellish the species accounts in Chapter 3 are beautiful renditions, although occasionally stylized to the point of minor inaccuracies, such as the Black Phoebe's (*Sayornis nigricans*) shortened tail. It is obvious that some of the drawings are intended as joyful celebrations (usually a species is represented from each major group) that add spice to the rich narrative.

Although a sturdy shelf, desk, and lap are necessary for this large book, it will serve well the professional, student, birder, and oth-

ers interested in Oregon's avifauna. I highly recommend it as a thorough regional reference.—ROBERT I. FREY, Klamath Bird Observatory, Ashland, Oregon; e-mail: bif@klamathbird.org.

CONSERVING BIRD BIODIVERSITY: GENERAL PRINCIPLES AND THEIR APPLICATION. Edited by K. Norris and D. J. Pain. Cambridge University Press, Cambridge, United Kingdom. 2002: 337 pp. \$100.00 (cloth), \$38.00 (paper).—In the preface, the editors state that the goal of this book is to bridge the gap between textbooks focused on general principles of conservation biology and the practical techniques used by avian conservationists. The target readership is broad; the book is designed as an entrée to the literature, as well as an up-to-date review for graduate and advanced undergraduate students, researchers at all levels, and policy-makers. The 900+ references associated with the 12 chapters will certainly benefit any reader. Topics progress from defining avian biodiversity (Chapter 1) and reasons to conserve it (Chapter 2), to monitoring bird populations (Chapter 3) and setting conservation priorities for species and sites (Chapters 4 and 5). Chapter 6 emphasizes critically imperiled birds. Chapters 7–10 focus on diagnosis and causes of population declines. The book closes with discussions on the interface between research, education, and teaching (Chapter 11) and the policies and programs affecting birds (Chapter 12). The chapters have little overlap and the book advances nicely with few typographical errors (although citing www.birdlife.org as www.birdlite.org in Box 5.3 did strike my sense of humor). The chapters provide topical overviews with additional details in tables, figures, footnotes, and text boxes. The text boxes, which contain useful information or interesting case studies, are a feature of the book that I enjoyed greatly.

The majority of the 19 contributing authors hail from the United Kingdom, or its former Eastern Hemisphere colonies, and many of the highlighted examples are from these areas. From my North American viewpoint, these examples added richness to the book. This richness, however, comes at the expense of

adequate coverage of avian conservation programs and issues in North, Central, and South America (the area of greatest avian richness); thus, American readers may not find mention of case studies or research programs familiar to them.

Although all of the chapters are relevant, I would have liked the editors to include a chapter on adaptive management (briefly mentioned at the end of Chapter 7). Presenting a case study of this current conservation/management paradigm could have benefited readers.

Overall, this book achieves its goals and could serve well as the basis for a course in avian conservation for graduate and undergraduate students, if supplemented with additional readings from the primary literature.—PAUL F. DOHERTY, JR., Colorado State University, Fort Collins, Colorado; e-mail: doherty@cnr.colostate.edu

AVES DE LA SABANA DE BOGOTÁ, GUÍA DE CAMPO (BIRDS OF THE SABANA DE BOGOTÁ, FIELD GUIDE). By F. G. Stiles, C. I. Bohórquez, C. D. Cadena, S. de la Zerda, M. Hernández, L. Rosselli, M. Kelsey, I. D. Valencia, and D. Knapp. Asociación Bogotana de Ornitología, Bogotá, Colombia. 2000: 276 pp., 16 color plates, 15 habitat photographs, 3 color maps. \$25.00.—This field guide deals with the approximately 200 bird species that have been recorded on the mountain plateau where Colombia's capital, Bogotá, is located. For those not familiar with the region, the Sabana de Bogotá forms part of Colombia's eastern Andean range, or Cordillera, at 2,550–2,600 m elevation. It is of international importance to bird conservation because it is, essentially, the only home to two globally threatened endemic species, *Rallus semiplumbeus* and *Cistothorus apolinari*, as well as to several threatened endemic subspecies. These taxa are largely restricted to the Sabana's marshland habitats or *humedales*, which formerly characterized much of the Sabana.

The lack of conservation attention to the Sabana de Bogotá over recent decades is a national and international disgrace. Most of its globally unique marshlands have been drained

for farmland and urban development; just a few small patches of such habitat subsist today. The few remaining *humedales* continue to be threatened by road-building programs, development of "country clubs" and other resorts, government-endorsed drainage for additional houses and urban development, as well as illegal encroachment. Andean forest is now restricted to just a few steep mountains bordering the Sabana. One bird species (Colombian Grebe, *Podiceps andinus*) and two subspecies (Yellow-billed Pintail, *Anas georgica niceforoi* and Bearded Tachuri, *Polystictus pectoralis bogotensis*) endemic to the Sabana and adjacent wetlands are already extinct; doubtless more will follow if government and industry continue to shun conservation of biodiversity.

The authors of *Aves de la Sabana de Bogotá* aim to raise awareness of conservation issues in Colombia's capital and surrounding region, to foster an interest in birds amongst Bogotá's people, and to educate them so that the mistakes of the past are not repeated. Conservation entities in Colombia have often ignored the sad realities of conservation mismanagement. It is, therefore, paradoxically refreshing to read the forward by William Eduardo Morales Rojas of Bogotá's government environmental agency, in which he draws attention to "the lack of an environmental ethic" amongst Bogotá's inhabitants. His foreword, an eloquent, clarion call to conservation action in the region, merits attention by politicians and other decision-makers.

Turning to the text itself, it is evident that this book is more than just a field guide. Much of the book (72 pages) is devoted to descriptions of the various habitats in the Sabana, a rationale for the book's publication, interpretative notes on species and bird taxonomy, and how to observe birds. There are, of course, books entirely devoted to "how to watch birds," but this is the first book written for Colombians in Spanish that covers topics such as how to watch and observe birds, how to "pish," and what to look for when choosing binoculars. This book provides a good and concise summary, although at times veers toward the patronizing; for example, apparently, a 12-year-old should be expected to identify only 25 or so species. By comparison, my own life list at that age was about 180 (in

Europe, not the tropics), and this is not exceptional.

The various species accounts appear to have been based on translations of Hilty and Brown's accounts in *Birds of Colombia*, and then embellished with much additional ecological and Sabana-specific information gleaned from the authors' field experiences. The species accounts are accurate and interesting, and include information on identification, vocalizations, habitats, nesting, status in the Sabana, overall geographical and elevational distribution, and various additional notes on taxonomy or ecology. More than 50 species of vagrants, accidentals, or birds that typically occur only in the margins of the Sabana are treated in short notes; most of these species are not illustrated, however. Localities in which species have been recorded, or can be regularly encountered, and species' abundances in different habitats of the region are detailed. The species accounts are extremely well-written, concise, and accurate, as one would expect from publications by Gary Stiles and his team.

Generally, the plates are good, and in most cases should suffice for identification purposes among both beginning and advanced users of the book. The illustrations of Nearctic migrants, in particular, mark a fresh and welcome change from many other significant Neotropical ornithological publications in recent years; the plates of these species are among the book's best and most accurate. However, the plates depicting the waders are blurred, and plates of some groups, such as nightjars and tapaculos, appear dull, vaguely defined, or washed out.

Who will find this book appealing? As a basic introductory text to birds in Bogotá, *Guía de las Aves en el Jardín Botánico* by Enrique Zerda Ordoñez describes and illustrates most species one is likely to encounter in Bogotá. For those interested in going further afield, one formerly had to understand English and use Hilty and Brown's *Birds of Colombia*. *Aves de la Sabana de Bogotá* replaces *Guía de las Aves en el Jardín Botánico* as the leading text for the region. It is likely that publication of *Aves de la Sabana de Bogotá* was due, in part, to frustration with the 16+ year delay in publishing the translated version of *Birds of Colombia* (*Aves de Colom-*

bia). Now that *Aves de Colombia* is published, one wonders how much *Aves de la Sabana* will be used in the field, as *Aves de la Sabana de Bogotá* is restricted to a very narrow elevational and geographical range. Outside of the *humedales*, perhaps the most accessible and high-quality bird habitat near Bogotá is Reserva Natural Chicaque, 45 min south of the city by bus. Although a species list for Chicaque is included, and there are various in-text references to it, several species found there are not illustrated or described fully, as they do not occur in the Sabana *sensu strictu*. Thus, a Bogotá-based newcomer to the world of birding is likely to outgrow *Aves de la Sabana de Bogotá* rather quickly. Perhaps this outcome is inevitable when one considers Bogotá's geographical position and transport links: within a 2-hr drive, one could be birding in the hot, dry Magdalena Valley or Colombia's eastern plains, and, within a short flight one could be in any of three Andean cordilleras, the Chocó, the Carribean, or the Amazon.

Despite its geographical limitations, *Aves de la Sabana de Bogotá* will serve as an exemplary text for beginning birdwatchers through students to expert ornithologists in Colombia's capital. Let us hope that, because of this book, more Colombians are encouraged to take an interest in birds, and to work actively toward the conservation of Bogotá's threatened endemic bird species and their habitats.

In addition to being an important reference in its own right, the detailed summaries of species ecology and distribution in *Aves de la Sabana de Bogotá* will be of interest to all who work with Colombian and other South American birds. *Aves de la Sabana de Bogotá* is thorough, contains a wealth of interesting and useful information, and is reasonably priced. Hopefully, it will give Colombia's amazing birds a wider national following, and bring conservation issues to the forefront of decision-making in the Bogotá region.—THOMAS DONEGAN, ProAves Foundation, Reading, United Kingdom; e-mail: foundation@proaves.org

A CONCISE HISTORY OF ORNITHOLOGY. By Michael Walters. Yale University Press, New Haven, Connecticut. 2003: 255

pp., 93 black-and-white figures. \$30.00 (cloth).—Written by a British ornithologist, this book describes people and their ideas from a classical world perspective, including not only the advances, but the backwaters and diversions that delayed the progress of ornithological thought. It is written in a pleasant, narrative style and has a substantial reference list. The book's themes include tragic losses of specimens before they could be described for science; the medical training of the majority of the observers (although Walters fails to mention that William Turner was a physician); and new descriptions of species by men such as Pennant and Latham, after whom species were not named due to their delay in adopting the Linnaean system of binomial classification.

Walters seems obsessed by systems of classification, and although no book that highlights centuries of history can be perfect, he uses 70 pages to list (only roughly in chronological order) classifications devised by 30 different authors. Perhaps the Index is representative of his obsession; for some taxonomic authorities, it lists the page of the classification but not the page where species' authority is discussed. Walters begins with Walter Charleton, who in 1668 classified birds as Land or Water birds, and then, by what they ate and whether they sang; his sequence began with eagles and ended with cranes. Walters chose Hans Gadow as his 30th and final authority, whose 1892 classification approaches that of current systems, beginning with ratites and ending with Passeriformes. Surprisingly, American sequences, such as those of Elliott Coues and Alexander Wetmore, and the seven consecutive check-lists of the American Ornithologists' Union, receive no mention whatever. In addition, Walters categorizes Anton Reichenow's system, developed in 1914, as "absurd . . . never used by any ornithologist" yet that is the sequence followed worldwide by the decimalized library system.

The main advantage of Walter's book over the much longer, out-of-print, 1951 book by Stresemann, (translated into English in 1975 as *Ornithology from Aristotle to the Present*) is the numerous portraits of ornithologists that he included. One advantage of Stresemann's book is his scholarly use of footnotes and endnotes, which Walters' book lacks. Stresemann

also explains that Emperor Fredrick developed his attraction to ornithology through the "noble art of falconry," while Walters categorized the man as the first "thinker of significance" in ornithology.

Walters' historical treatment is accurate, yet at times differs from that of Stresemann. Stresemann fails to mention Johannes de Cuba, who published the first printed book with bird illustrations at Mainz in 1475, and Walters omits Theodorus Gaza, who translated *The History of Animals* from Greek into Latin in 1476. Stresemann overlooked Nehemiah Grew, who used binomial Latin names for birds and named the Gannett, *Anser bassanus*, in *Museum Regalis* in 1681. Both authors give short shrift to Linnaeus; in fact, Walters characterized Linnaeus' contributions to ornithology as "almost paltry" compared to those of Brisson and Buffon.

Even those who own Stresemann's book may wish to add Walters' to their collection—for its readability, illustrations, availability, and relatively low price. It provides a wonderful opportunity to learn about a large number of interesting and innovative people, whose names are retained in check-lists as describers of new species, or who made other contributions to our knowledge about birds. Buy a copy for yourself and another for your department or museum library.—C. STUART HOUSTON, University of Saskatchewan, Saskatoon, Canada; e-mail: houstons@duke.usask.ca

THE HISTORY OF ORNITHOLOGY IN VIRGINIA. By David W. Johnston. University of Virginia Press, Charlottesville, Virginia. 2003: 219 pp., 25 black-and-white illustrations, 7 tables. \$35 (cloth).—Virginia, known as the birthplace of North American ornithology, has a long and rich history in ornithology, with bird reports dating back to colonial times. *The History of Ornithology in Virginia* traces this rich history—from 65 million-year-old fossil birds, to the visits of such luminaries as Mark Catesby, Alexander Wilson, and Audubon, to the present.

The book contains 12 chapters, the first describing fossil evidence and the observations of 16th Century Native American peoples, who

created cave paintings of birds and used birds for decoration, clothing, and food. The second chapter describes 16th Century reports of Europeans who traveled to Virginia; it includes photographs of the first paintings of North American birds by John White, and one of the first lists of North American birds compiled by Thomas Hariot. Both White and Hariot were members of Sir Walter Raleigh's expeditions. Also included are Captain John Smith's descriptions of Virginia birds. Chapter 3 deals with 17th Century bird lists, explorers, and naturalists, including John Banister and John Clayton. Chapter 4 traces the 18th Century history of Virginia ornithology, including the reports and correspondence of Mark Catesby and other naturalists that led to international recognition of Virginia's bird life. Chapter 5 recounts activities of 19th Century collectors, development of local bird lists, and ornithological reports by Alexander Wilson, Audubon, Thomas Nuttall, and Thomas Jefferson (who compiled a list of all known Virginia birds).

Chapter 6 focuses on contributions made by members of the Smithsonian Institution and federal government in the 19th and 20th centuries, including Spencer F. Baird, Thomas Burleigh, Elliot Coes, Arthur Howell, Waldo McAtee, C. Hart Merriam, Harry Oberholser, Robert Schufeldt, and many others. Chapter 7 describes in detail several special places that are rich in birds, including the Great Dismal Swamp, Shenandoah Valley, and the Virginia Eastern Shore. Chapter 8 includes a history of the conservation movement—in particular, the emergence of game laws and the development of organizations such as the Virginia Society of Ornithology and the Virginia Department of Game and Inland Fisheries.

Chapter 9 concentrates on bird artists such as Edward Toppell, John Abbot, William Bartram, Alexander Wilson, and Audubon, as well as more recent artists—Francis Lee Jaques, Walter Weber, and Roger Tory Peterson, all of whom either lived in, or visited, Virginia. Chapter 9 also reviews the ornithological activities of several presidents of the United States (e.g., Theodore Roosevelt's 1907 observation and report of Passenger Pigeons, *Ectopistes migratorius*). Chapter 10 deals with extirpated and non-native species, including the Passenger Pigeon, Carolina Par-

akeet (*Conuropsis carolinensis*), and Trumper Swan (*Cygnus buccinator*). Chapter 11 concerns raptors and banding, including an account—about Mitchell Byrd and others—on the reintroduction and recovery of Peregrine Falcons (*Falco peregrinus*) and Bald Eagles (*Haliaeetus leucocephalus*) following the DDT disaster. The final chapter discusses Virginia ornithology in the 20th Century, and includes brief biographies of more than a dozen ornithologists who made important contributions. The chapter also highlights significant ornithological accomplishments and published bird lists and books. The book's appendices include Algonquian Indian bird names, principal bird collectors (compiled by Roger Clapp), and a bibliography of nature writings from Virginia. The references are extensive and a valuable resource for those interested in Virginia's natural history.

This book is well written, jargon-free, and nicely illustrated. It is a welcome addition to the literature on the history of ornithology—especially because Virginia has been so important in the long and prominent history of North American ornithology.—WILLIAM E. DAVIS, JR., Boston University, Boston, Massachusetts; e-mail: wedavis@bu.edu

PERU: THE ECOTRAVELLERS' WILDLIFE GUIDE. By David L. Pearson and Les Beletsky, with contributions by Martha L. Crump. Illustrations by Priscilla Barrett, David Beadle, David Dennis, Daniel Lane, John Meyers, Colin Newman, David Nurney, John O'Neill, and John Sill. Academic Press, San Diego, California. 2001: 502 pp., 99 color fauna plates with detailed legends, 13 color figures (12 flora and 1 fish), 30 color photographs (21 habitat and 9 fauna), 3 maps, and 1 table. \$29.95 (paper).—This nicely sized (5.5 × 8.5"; 1.5 lb.) *Ecotravellers' Wildlife Guide* (hereafter *Ecotravellers' Guide*) is a must in the suitcase of anyone traveling to Peru to observe nature. The highlight for any birder is the 61 plates of beautifully painted birds of 324 different species, many illustrating both sexes and some illustrating immatures. The true ecotraveller, however, also will appreciate the 8 plates of amphibians (39 species), 11 plates of reptiles (48 species), 15

plates of mammals (73 species), and 4 plates of arthropods (29 species).

Last August, while I was traveling in Peru, this guide was a constant reference for all my observations. We visited the coast (Paracas National Reserve), Andes highlands (Cusco and Machu Picchu areas), and the Amazon lowlands (Manu National Park). I recorded 139 bird species and found that 96 (69%) were illustrated in the *Ecotravellers' Guide*. My colleague, Peter Osenton, who is a better bird observer and spent more time birding, recorded 242 bird species, 131 (54%) of which were in the *Ecotravellers' Guide*. For more serious birders like Peter, the *Field Guide to Birds of Peru* (hereafter *Birds of Peru*) by James F. Clements and Noam Shany is certainly recommended. However, many of the other naturalists with our group appreciated the simpler *Ecotravellers' Guide* and, therefore, were not too overwhelmed by the large number of species Peru has to offer.

Although the *Ecotravellers' Guide* is a great all-purpose natural history guide to many species, the more advanced *Field Guide to Birds of Peru* is especially advantageous for serious birders dealing with large families or genera, such as hummingbirds and tanagers. The *Ecotravellers' Guide* illustrates 21 species of hummingbirds and 23 species of tanagers, whereas the *Birds of Peru* illustrates an amazing 135 species of hummingbirds and 92 species of tanagers. Several individuals in our group, however, thought that some of the bird illustrations in the *Ecotravellers' Guide* were of better quality and more accurate than those in the *Birds of Peru*.

The legend on the page opposite each plate briefly describes each illustrated species and its habitat; it also provides an icon(s) that identifies the region where the species may be expected, and the species' scientific name. This was especially helpful when we encountered familiar species, such as Black Skimmer (*Rynchops niger*) and American Oystercatcher (*Haematopus palliatus*), and wanted to be sure that it was, indeed, the same as the North American species and not another species with the same common name.

The *Ecotravellers' Guide* does not illustrate some of the more familiar North American species, such as the Pied-billed Grebe (*Podilymbus podiceps*), Wood Stork (*Mycteria*

americana), Cinnamon Teal (*Anas cyanoptera*), and American Kestrel (*Falco sparverius*), but it does illustrate other common North American species, such as Osprey (*Pandion haliaetus*), Great Egret (*Ardea alba*), Spotted Sandpiper (*Actitis macularia*), and Swallow-tailed Kite (*Elanoides forficatus*).

Our group identified 10 primate species, 6 of which were in the Ecotravellers' Guide. We also saw four other mammals and four reptiles, with three of the mammals and all four reptiles illustrated in the Ecotravellers' Guide. No amphibians or arthropods illustrated in the guide were seen on the trip.

The first four chapters of the book give the reader a good basis for understanding ecotourism, the geography and habitats of Peru, the Peruvian parks and reserves available for nature observation, and the ecology and natural history of Peru. Chapters 5 and 6, edited by Martha Crump, provide a scholarly discussion of amphibians and reptiles. Chapters 7 and 8 discuss birds and mammals, and Chapter 9 features insects and other arthropods.

In addition to the text for each group of animals, the authors also provide erudite "close-up" sections on natural history topics pertinent to Peru. These topics include (1) *Why is farming so difficult in the tropics?* (2) *Frog population declines*, (3) *Endemism and high species diversity: why Peru?* (4) *Frugivory: animals that eat fruit and the trees that want them to*, and (5) *Of kingfishers and competition: big bills and little bills and how they got that way*.

The detailed text for each wildlife group includes a discussion about its natural history,

breeding ecology, and population status. Information is presented on why parrots eat clay (geophagy) at the famous "clay lick" along the Madre de Dios River, and that the Screaming Piha (*Lipaugus vociferans*) is the bird species we often hear in the background of jungle movies. The piha is extremely hard to see; we never saw any despite hearing them on numerous occasions directly overhead in the open canopy of Manu National Park.

The last chapter of the Ecotravellers' Guide includes an important eight-page message regarding the conservation work of the Wildlife Conservation Society (the book's sponsor) in Latin America, followed by an appeal to join the Society. The index is divided into two sections, one for wildlife species and one for general subjects. I noted only a few minor errors.

Birdwatching in Peru is an exciting experience that can be improved greatly by using the Ecotravellers' Guide. When birders hear such exotic names as Black-capped Donacobius (*Donacobius atricapillus*), Peruvian Seaside Cinclodes (*Cinclodes taczanowskii*), and Chestnut-eared Aracari (*Pteroglossus castanotis*), they will be reaching for this book to get a look at these strangely named species. I highly recommend *Peru: The Ecotravellers' Wildlife Guide* for all ecotravellers visiting Peru, although I also advise the advanced birder to pack a copy of *Field Guide to Birds of Peru* for identifying the more difficult, and less common, species not included in the Ecotravellers' Guide.—MATTHEW C. PERRY, USGS Patuxent Wildlife Research Center, Laurel, Maryland; e-mail: matt_perry@usgs.gov

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FRONTISPIECE. Mealy Parrots (*Amazona farinosa*), Blue-headed Parrots (*Pionus menstruus*), and Orange-cheeked Parrots (*Pionopsitta barrabandi*) at the clay lick (geophagy site) near the Tambopata Research Center in southeastern Peru. Brightsmith (p. 134) reports that lick use was highest on sunny mornings and that inclement weather reduced geophagy. When early morning rain prevented birds from using the lick, they did not return later in the day nor did they compensate for rainy mornings by increasing lick use on subsequent days. Original oil painting by Barry Kent MacKay.

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THE COGNITIVE FACE OF AVIAN LIFE HISTORIES

The 2003 Margaret Morse Nice Lecture

ROBERT E. RICKLEFS¹

ABSTRACT.—Cognition includes the acquisition, processing, retention of, and acting upon information from the environment. Avian cognition has been investigated by the approaches of experimental psychology and in the context of specific tasks, such as spatial memory. However, the costs and benefits of cognitive ability have not been considered in a life-history context. I explore possible relationships between behaviors that might indicate cognitive function and other attributes, particularly brain size, rate of development, age at maturity, and life span. Large brain size and prolonged development are seen as potential costs of intelligent behavior. Long life span may permit the extended learning periods that support experienced-based cognitive function. Play behavior, which plausibly supports the development of motor and social skills, and, to a lesser extent, foraging innovations, are related to brain size. The challenge of foraging in a spatially and temporally varying environment, experienced for example by pelagic seabirds, is associated with prolonged embryonic development. Although these connections lack mechanistic foundations, they suggest that cognition can be considered as a part of the life history of the individual and that potential costs of cognition might provide guidelines for directing the comparative study of intelligent behavior. *Received 30 April 2004, accepted 7 June 2004.*

Over the course of her remarkable career, Margaret Morse Nice produced many original contributions to ornithology, including her pioneering studies on the life histories of birds (e.g., Nice 1937, 1943, 1957) and the development of behavior (Nice 1962). For many of us who were students during the 1960s, which was a period of transformation in ecology and behavior, her work laid the foundation for all that we set out to accomplish. It is this intersection of life history and behavior that I would like to address in this contribution. I am grateful to the Wilson Ornithological Society, and particularly to Jed Burt, for giving me the opportunity (and a captive audience) for exploring ideas that have fascinated me for many years, but which have not come into clear focus until now.

Behavior provides the individual a flexible

relationship with its environment. The environment of every organism is varied in space and changes constantly through time, often unpredictably, but also with regularities that can be learned over time. Individuals respond to their environments in a variety of ways. Many behaviors are “hard-wired” into the nervous system and express evolved responses, available from birth, to consistent features of an individual’s surroundings. At the other extreme, organisms occasionally encounter novel situations for which they must devise novel solutions, what many of us would consider intelligent behavior. We suspect that species vary widely in terms of what we think of as intelligence; most ornithologists, if asked, would put parrots and corvids at the top of the avian intelligence scale and relegate doves and sparrows to lower positions, although one could argue that individuals of every species handle very well the tasks necessary for their survival and reproduction.

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I assume that most behavior is adaptive and contributes to the lifetime reproductive success, or fitness, of the individual. Variation in capacities for certain types of behavior presumably reflects different balances between the costs and benefits of such behavior in the context of demands of the environment. I also assume that the capacity to think is costly, at least in terms of the development and maintenance of the hardware required, and that if it is not necessary to think in a particular way, individuals should not bear the cost of that particular ability. This simple idea constitutes a life-history approach, which considers the conflicting contributions of adaptations to fitness resulting from the allocation of limited time, energy, tissue, and other resources. I find it remarkable that the evolution of intelligent behavior is rarely considered within a life-history framework. Indeed, one of the most widely respected textbooks in animal behavior that uses an evolutionary approach (Alcock 1998) does not list cognition in its index and under intelligence refers only to a single page devoted to the heritability of IQ.

In this essay, I have endeavored to treat thinking, or the capacity to think, in a life-history context. The fact that some birds appear to do less "thinking" than others suggests that thought might have substantial costs or that it might be highly constrained by other aspects of the life history. Of course, thought is hard to measure. It is possible, however, that some of the costs it incurs are not. These costs might involve maintaining a large brain and prolonging development to build a large, complex nervous system and acquire the experience necessary to perceive pattern in environmental variation. If this inference were correct, could we not use these presumed costs to indicate certain mental capacities? I shall use data on brain mass and the length of the incubation period for a large number of birds to construct a two-dimensional space representing some presumed costs of cognition. I will then determine whether certain kinds of behavior that are associated with cognitive ability (sociality, appearance of novel behaviors, play, experience-based foraging, for example) bear a relationship to presumed costs (some do!). Of course, patterns do not tell the whole story. However, we can use patterns to guide our thinking about thought in a

life-history context. Clearly, this is a crude beginning to a highly complex and difficult task. I hope, however, that this essay will encourage readers to regard intelligent behavior as integral to the life history of the individual and subject to selection that weighs its costs and benefits.

WHAT IS COGNITION?

According to Shettleworth (2001), cognition, broadly defined, "includes perception, learning, memory and decision making, in short all ways in which animals take in information about the world through the senses, process, retain and decide to act on it." Vauclair (1996:10) sees cognition more narrowly as allowing an individual "to adapt to unpredictable changing conditions in its environment. Thus, behaviors that would aid adaptation would reflect several characteristics, such as *flexibility*, *novelty*, and *generalization*. Flexibility of behavior designates the possibility of constructing an adapted response to unusual external conditions. The response also must be novel in the sense that it does not express the existence of a pre-wired program. Finally, the novel behavior, established to solve a novel problem, must be susceptible to generalization to situations that differ partially or totally from those in which they were initially acquired."

Many psychologists distinguish "between cognition, a possible means to an end, and intelligence, an assessment of performance judged by some functional criteria" (McFarland 1989:130). Intelligent behaviors are often regarded as specific adaptations to specific problems (Rozin 1976). For example, the sophisticated navigation abilities of pigeons appear to be highly intelligent (Wiltschko and Wiltschko 1993, 1998; Walcott 1996; Wallraff 2001), but because they are mostly controlled by hard-wired systems, these abilities cannot be generalized to other kinds of behavior. Thus, by Vauclair's definition, they cannot be considered as an indication of general cognitive ability. It is entirely possible that intelligence and cognition defined in this manner represent points on a continuum and that the distinction, although perhaps heuristically useful, is artificial. Cognitive abilities themselves are certainly specialized in many respects. For example, Clark's Nutcrackers (*Nucifraga col-*

umbiana) have a high degree of spatial cognition across many types of tasks, but perform less well with non-spatial information, such as color (Olson et al. 1995).

I shall adopt a broader definition of cognitive ability here to include the acquisition and processing of information from the environment as a basis for behavior. I hasten to add that the study of animal cognition is not the study of animal consciousness, although consciousness (self-awareness) should be considered as a type of cognitive behavior (Rozin 1976; Griffin 1984, 1985; Terrace 1984; Roitblatt 1987; Bekoff 2000).

Many researchers regard as central to cognition the concept of a cognitive map (Roitblatt 1982, 1987; Gallistel 1990; Gervet et al. 1996). Animals acquire and remember landmarks, attach values to them, and incorporate changes in these landmarks over time. Cognitive maps may represent physical space (Kamil and Jones 1997, Gibson and Kamil 2001), or they may relate to social "space," predator "space," weather "space," and the like. A cognitive map is a representation of features of the world in the brain itself, and neurobiologists are beginning to discover the correspondence between the two (e.g., Jarvis and Mello 2000, Bingman and Able 2002).

HOW DO WE ASSESS COGNITIVE ABILITIES?

Corvids and parrots are generally regarded as intelligent and sociable (Takahashi and Keller 1994; Hunt 1996; Marler 1996; Cohen et al. 1998; Pepperberg 1999, 2002; Bugnyar et al. 2001; Balda and Kamil 2002; Bugnyar and Kotrschal 2002; Heinrich 2002; Hunt et al. 2002; Knudsen 2002). What does this mean? We have various tools for probing the cognitive abilities of animals. The most important of these comprise the methods of experimental psychology, in which mental capacities are assessed by performance in various kinds of behavior tests. A second approach, which may have broader application in comparative studies, is to record behavioral correlates of cognitive ability. Recently, the frequency of behavioral innovations has received attention in this regard (Lefebvre et al. 1997, 1998; Nicolakakis and Lefebvre 2000) and particular cases, such as tool making in New Caledonian Crows (*Corvus moneduloides*; Hunt 1996,

Chappell and Kacelnik 2002, Hunt and Gray 2002, Weir et al. 2002), have received considerable and well-deserved attention in the media. A third approach is to infer cognitive abilities from the kinds of problems that animals have to solve in their daily lives. That is, we can ask what kinds of mental function are needed for an individual to behave the way it does in its particular environment. For example, tracking nectar sources by hummingbirds (Garrison and Gass 1999, Bateson et al. 2003) and cache retrieval by jays (Balda et al. 1996; Griffiths et al. 1999; Clayton et al. 2001, 2003; Balda and Kamil 2002) may require more sophisticated spatial and temporal representations than leaf gleaning by warblers and ground foraging by doves.

Representation, which might be thought of as the formation of mental images, can be verified in its simplest form by various tests of memory (e.g., Griffiths et al. 1999, Clayton et al. 2001). Beyond this, experimental comparative psychology investigates problem-solving abilities associated with concepts of sets, identity and oddity, perceptual categories, serial learning, and imagery (Vauclair 1996). In an experimental setting, identifying the formation of sets, for example, involves a subject's ability to generalize the concept of similarity to novel objects; serial learning is revealed by the ability to construct a correct sequence out of a subset of sequentially presented stimuli; and so on. Many excellent reviews detail the results of experimental psychology (Pearce 1987; Gallistel 1989; Ristau 1991; Byrne 1994; Balda et al. 1996, 1998; Vauclair 1996; Shettleworth 1998; Griffiths et al. 1999; Pepperberg 1999; Heyes and Huber 2000; Clayton et al. 2001; Wynne 2001; Bekoff et al. 2002).

In a comparative, life-history framework, the approaches of experimental psychology become laborious and context dependent. For example, it is difficult to compare the results of psychological tests on species with varied communication modalities and different problem solving requirements in their lives. Therefore, the analyses in this discussion rely on various presumed behavioral correlates of cognitive function and inferences concerning cognitive function from the behavioral demands posed by tasks that organisms accomplish in their daily lives.

COGNITION AS A LIFE-HISTORY TRAIT

The benefits of cognition.—The value of cognition must involve functioning in a complex, variable environment where decisions conditioned by experience or reasoning are crucial. As explained by W. J. Smith (1990), cognitive function enables prediction and shapes expectation about the environment, including social interactions (see also Stephens 1989). Examples include food caching (Krebs et al. 1996, Gibson and Kamil 2001, Kamil and Cheng 2001), risk assessment associated with variable rewards (Real 1991, 1993; Kacelnik and Bateson 1996; Bateson and Kacelnik 1997; Garrison and Gass 1999; Marsh and Kacelnik 2002; Schlick-Paim and Kacelnik 2002), context-dependent responses to social signaling (W. J. Smith 1990), social negotiation based on shared information (Smith 1997, 1998), and reciprocal altruism depending on long-term association with identifiable individuals (Trivers 1971, Axelrod and Hamilton 1981).

The costs of cognitive ability.—The association of well-developed cognitive abilities with a large brain may be a particularly human conceit, but many studies of differences in behavior among species are generally consistent with such a relationship (Jerison 1973, Clutton-Brock and Harvey 1980, Macphail 1982, Dunbar 1992) and certain measured cognitive abilities are related to the size of relevant parts of the brain. I am referring in particular to the relationship between spatial memory and the size of the hippocampus (Healy and Krebs 1996, Biegler et al. 2001), but similar structure-function connections are evident with respect to other behaviors, such as singing, and related brain regions (Brenowitz et al. 1985, Brenowitz and Arnold 1986, Devoogd et al. 1993, Bernard et al. 1996), although one must exercise caution in generalizing such connections (Aboitiz 1996, 2001).

The brain is thought to be an expensive organ metabolically (Field et al. 1939, Martin and Fuhrman 1955, Aiello and Wheeler 1995) and large brain size presumably also applies architectural stresses on morphology and aspects of animal function (Aboitiz 1996). Flight itself may impose some limits on brain size. Another cost of a larger brain or more precise and complex neural connections with-

in the brain may be prolonged development. The basic architecture of the brain and most of its growth occurs before birth in mammals (Pagel and Harvey 1988), and this is also true in birds (Portmann and Stingelin 1961; Starck 1993, 1998; Ricklefs and Starck 1998). Birds exhibit tremendous variation in the length of the incubation period—more than a factor of three when incubation period is normalized by egg size (Ricklefs 1993). Costs of prolonged incubation include increased exposure to time-dependent mortality, higher energy requirements of embryonic growth, and increased reproductive stress for parents. The benefits of long incubation periods have not been identified, although presumably they reflect a higher quality chick (Ricklefs 1992, 1993).

A more cognitive life style might also be associated with a long learning period to acquire information, leading to delayed reproduction and reduced lifetime reproductive success. For example, increased cognitive ability might carry with it the opportunity to exploit a type of food supply that is not available, or is less efficiently used, without acquiring extensive information about temporal and spatial distribution of prey or of suitable foraging conditions. Complex social settings may require learning appropriate responses to individual variations in behavior and signaling.

CAN WE RECOGNIZE COGNITIVE ABILITIES BY THEIR ASSOCIATED COSTS?

I believe that the most obvious candidates for costs are brain size and embryonic development period. Postnatal growth rate and age at maturity are also reasonable choices in that they reflect a substantial portion of brain growth and development and the most significant part of an individual's learning period. In fact, these measures are generally correlated with embryonic development.

The relationship between brain mass and body mass in birds is shown in Figure 1. The residuals from the logarithmic regression provide a body mass-specific index to relative brain size. Averaged over larger taxonomic groups of birds (Sibley and Monroe 1990), these residuals identify several families with larger-than-average brain mass: Psittacidae, Strigidae, Corvidae, Picidae, Bucerotidae. It is not surprising to find the parrots and corvids

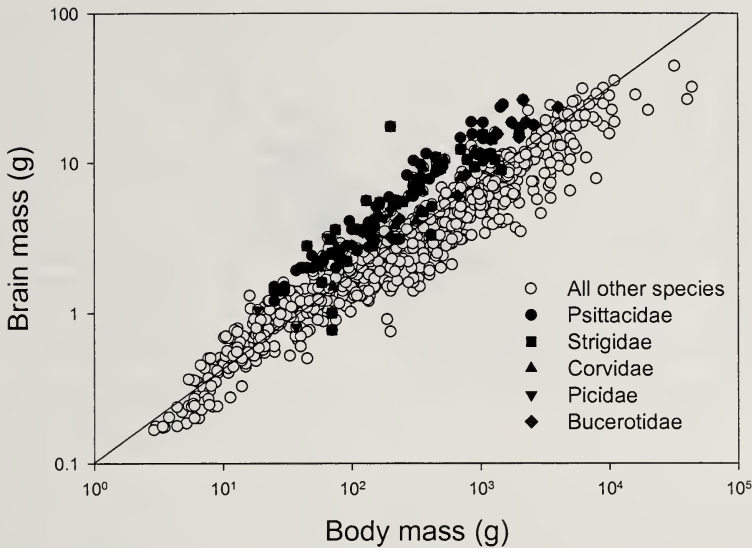


FIG. 1. Relationship between brain mass and body mass in birds based on data for 837 species in 104 families (for details, see Nealen and Ricklefs 2001). Regression within orders ($n = 23$) $F_{1,780} = 6590$, $P < 0.001$, slope = 0.625 ± 0.008 , intercept = -0.997 ; thus, the equation is $\log \text{brain} = -0.997 + 0.625 \times \log \text{body}$. $R^2 = 0.952$, RMSE (within orders) = 0.114. Order effect: $F_{22,780} = 48.8$, $P < 0.001$. Residuals are calculated from this regression line. Among families represented by more than 10 individuals, those with the highest residual brain masses were Psittacidae (0.27 ± 0.10 SD, $n = 49$), Strigidae (0.25 ± 0.17 , $n = 24$), Corvidae (0.24 ± 0.10 , $n = 21$), Picidae (0.22 ± 0.11 , $n = 13$), and Bucerotidae (0.15 ± 0.07 , $n = 13$). Those with the lowest residuals were Phasianidae (-0.30 ± 0.11 , $n = 39$), Columbidae (-0.22 ± 0.10 , $n = 21$), Anatidae (-0.14 ± 0.09 , $n = 64$), Scolopacidae (-0.12 ± 0.05 , $n = 27$), and Trochilidae (-0.12 ± 0.06 , $n = 27$).

near the top of the list, and hornbills are also known for complex social behavior (Kemp 1995), which might be indicative of well-developed cognitive abilities. Owls have very sophisticated foraging methods involving complex processing of auditory information (Takahashi and Keller 1994, Cohen et al. 1998, Knudsen 2002). I must have underestimated woodpeckers in the past, although Acorn Woodpeckers (*Melanerpes formicivorus*) certainly exhibit complex social behavior (e.g., Koenig and Mumme 1987, Koenig et al. 1998). Families on the bottom of the list of relative brain size are Phasianidae, Columbidae, Anatidae, Scolopacidae, and Trochilidae. It is notable that three of these groups have precocial offspring whose brains are well developed at hatching (Ricklefs and Starck 1998). It may also be significant that four of these groups constitute the bulk of bird species that have been hunted commercially and for sport.

The relationship between incubation period and egg mass in birds is shown in Figure 2. Again, residuals from the logarithmic regres-

sion provide an index to relative incubation period. In this case, taxa with exceptionally long incubation periods include Procellariiformes, Accipitridae, Spheniscidae, Psittacidae, Strigidae, Bucerotidae, and Falconidae. Three of these families also have exceptionally large relative brain size. In addition, the group includes two lineages of seabirds and most raptorial birds. On the low end of the scale are the Picidae, Columbidae, Fringillidae, Muscicapidae, and Passeridae, all of which have extremely altricial development and tend to have small body sizes.

Residuals from the brain mass and incubation period regressions define a space within which any particular group of birds can be placed. Within this space, the presumed cost of cognition increases with larger relative brain size and longer relative embryonic development, and this is where one expects to find birds with the most developed cognitive abilities. Because we have little direct comparative information on the cognitive capacities of birds, with the exception of pigeons, parrots, and corvids, I shall consider several

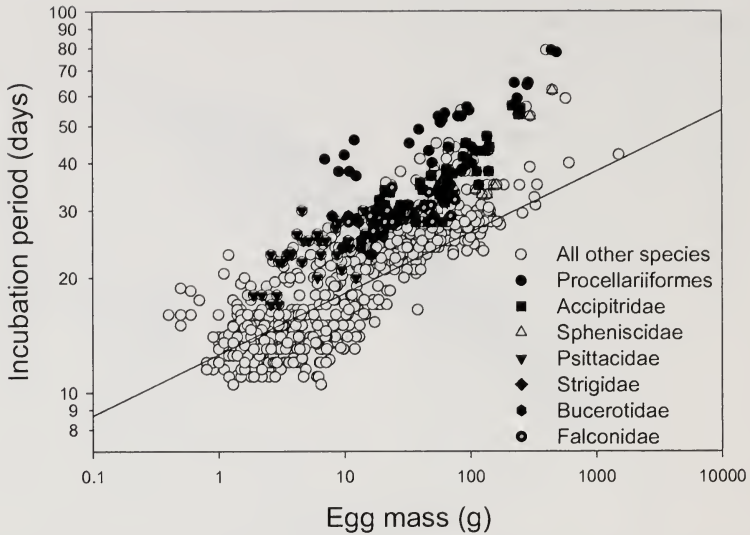


FIG. 2. Relationship between incubation period and egg mass in birds based on 799 species in 19 orders (for details, see Ricklefs 1993). Regression within orders ($n = 19$) $F_{1,776} = 203$, $P < 0.001$, slope = 0.160 ± 0.008 , intercept = 1.099 ± 0.073 ; thus, the equation is \log incubation period = $1.099 + 0.160 \times \log$ egg mass, $R^2 = 0.833$, RMSE (within orders) = 0.073. Order effect: $F_{18,776} = 35.1$, $P < 0.001$. Residuals are calculated from this regression line. Among taxa with exceptionally long relative incubation periods are Procellariiformes (0.323), Sulidae (0.239), Accipitridae (0.174), Trochilidae (0.172), Apodidae (0.156), Spheniscidae (0.153), Psittacidae (0.146), Strigidae (0.137), Bucerotidae (0.135), and Falconidae (0.135). Those with exceptionally short incubation periods include Sturnidae (-0.119), Picidae (-0.088), Columbidae (-0.067), Fringillidae (-0.053), Muscicapidae (-0.048), and Passeridae (-0.031).

behavior indices that might plausibly be related to cognition: (1) cooperative breeding; (2) sociality, or group living; (3) play behavior; (4) foraging innovations; and (5) challenging foraging situations. I shall also compare the putative costs to life span (which is also closely related to age at maturity) to assess the idea that some types of cognitive behavior require extensive learning periods.

Cooperative breeding.—My criterion for cooperative breeding for each family or other large taxonomic group is the proportion of species exhibiting helping behavior, reported by Jerram Brown (1987:table 3.1). The rationale for using cooperative breeding as an index to cognition is that in many family or extended family groups, individuals discriminate the recipients of helping behavior on the basis of relationship, which requires the learning of kin relationships (Emlen et al. 1995). The taxonomic groups with the highest proportion of helping, according to Brown's summary, are the hornbills, other coraciiforms, grebes, corvids, and mousebirds. Hornbills and corvids also get high scores for the putative costs of

cognition. In general, however, the proportion of species with helping behavior is unrelated to either relative brain mass or relative incubation period. In a stepwise multiple regression of the proportion helping (SAS PROC GLM), neither relative brain mass ($F_{1,20} = 0.46$, $P = 0.50$) nor relative incubation period ($F_{1,20} = 2.96$, $P = 0.10$) were significant effects (total $R^2 = 0.142$). In retrospect, helping behavior is probably not a good cognition index because, in essence, helping merely combines failure to disperse with what all birds with altricial development do naturally, that is, feed offspring.

A more pertinent index might be the capacity to develop complex interactions within and among extended family groups in species with social breeding, where reproductive success may hinge on personal knowledge of, and long-term association with, other individuals in the group. For example, among the species of cooperatively breeding birds detailed in Stacey and Koenig (1990), those engaging in colonial breeding belonged to coraciiforms

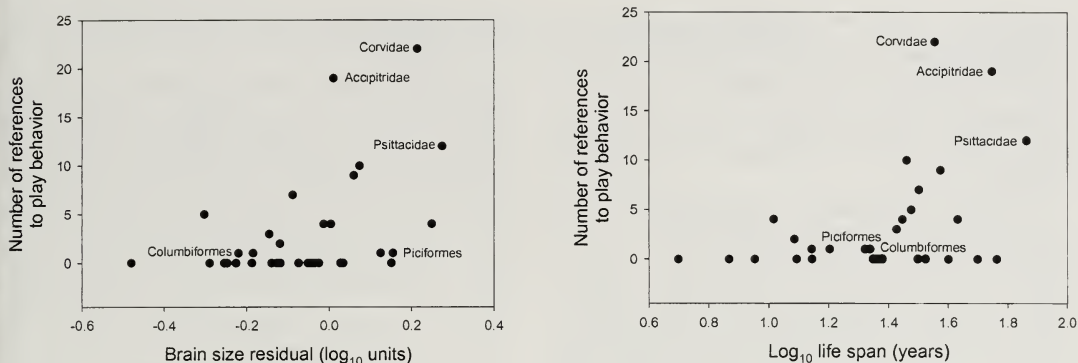


FIG. 3. Relationship between number of publications describing play behavior and relative brain size (left) and life span (right). From data compiled by Fagen (1981).

and corvids (J. N. M. Smith 1990:table 2), taxa with relatively large brains.

Sociality.—Group living balances benefits of group defense and social foraging against the costs of local competition for resources and social strife. Social behavior is thought by many authors to go hand in hand with cognitive behavior and brain size in primates (Sawaguchi 1990, 1992; Dunbar 1992, 1993). The “social complexity hypothesis” states that living in large groups selects for enhanced cognitive abilities with respect to recognizing individuals and assessing social relationships (Cheney and Seyfarth 1990, Byrne and Whiten 1997, Kummer et al. 1997). Support for this hypothesis has recently come from experimental studies on cognitive abilities in jays (Bond et al. 2003). My criterion for group living was the tendency to form groups with complex social structure. Both parrots and corvids place high on the list of such taxa, but to keep things simple I subjectively assigned taxa a score of either 0 or 1. Among the less social taxa are ducks, doves, cuckoos, quail, oscine passerines, and raptors; among the more social taxa are parrots, corvids, many seabirds, and many coraciiforms. Again, as in the case of helping behavior, group living was not a significant effect in an analysis of variance (ANOVA: SAS PROC GLM) for either relative brain mass ($F_{1,33} = 2.04$, $P = 0.16$, $R^2 = 0.058$) or relative incubation period ($F_{1,30} = 0.95$, $P = 0.34$, $R^2 = 0.031$). Nor did a discriminant analysis with body size, relative brain mass, and relative incubation period distinguish social versus non-social species ($F_{3,28} = 0.69$, $P = 0.57$). Different observers would

assign different scores, but the result probably would not change. Again, the problem with group living as an index to cognition is that many associated behaviors may require little more cognitive capacity than the kinds of cooperative and antagonistic interactions that all birds engage in, whether social or not. A better understanding of more complex behavior in social species based on individual knowledge and association might lead to a better index (e.g., W. J. Smith 1990, 1998), but this is beyond my understanding of bird societies.

Play.—Play is a more promising indicator of cognitive abilities because play presumably represents practice behaviors that refine physical and social skills (Fagen 1981, Byers and Walker 1995, Bekoff and Byers 1998). Unfortunately, there is no widely accepted definition of play in birds and comparative studies of avian play behavior are largely lacking. We all know play when we see it, but many reports of play in the ornithological literature are similarly anecdotal. I have taken as my index to play the number of publications describing play behaviors listed in Tables 3–26 to 3–28 of Fagen (1981). The taxa that come out on top of this list are falcons, passerids, parrots, accipiters, and corvids. The sample is undoubtedly biased by the large number of studies on these groups; however, it is noteworthy that each of these five taxa has above-average relative brain size (Fig. 3). The data were analyzed by a stepwise multiple regression, with body mass, relative brain mass (rbrain), relative incubation period, and life span as independent variables. In this analysis, brain size ($F_{1,26} = 7.0$, $P = 0.014$) and life

span ($F_{1,26} = 5.85$, $P = 0.023$) explained 37% of the variance in number of citations of play behavior. Relative brain size by itself explained 23% of the variance ($F_{1,27} = 8.1$, $P = 0.008$, $\text{play} = 4.42 [\pm 1.00] + 17.29 [\pm 6.08] \text{rbrain}$).

Foraging innovations.—Louis Lefebvre and his colleagues at McGill University have recently tabulated reports of foraging innovations from the literature. Lefebvre et al. (1997) define foraging innovation as “either the ingestion of a new food type or the use of a new foraging technique,” generally a behavior reported either for the first time or as being highly unusual for a given species. These include such diverse behaviors as an American Kestrel (*Falco sparverius*) drowning a Red-winged Blackbird (*Agelaius phoeniceus*), a Hooded Merganser (*Lophodytes cucullatus*) depredating an adult meadow vole (*Microtus pennsylvanicus*), and sparrows searching car radiator grills for insects. Here, I use as an index the proportion of papers on a particular taxonomic group that describe foraging innovations, compiled for North American and Australian birds by Lefebvre et al. (2001). Thus, this index is corrected for research effort. Incidentally, more than half of the reported innovations in North American birds come from the pages of *The Wilson Bulletin*, which remains one of the few ornithological journals that publishes natural history observations.

Lefebvre and his colleagues have shown that the incidence of foraging innovations is positively related to brain size (Lefebvre et al. 1997, 1998, 2001). My analysis also reveals such a relationship, although it is weak ($r = 0.38$, $P < 0.05$; arcsin-transformed: $r = 0.46$, $P = 0.016$, $n = 27$). The taxa with the highest incidence of reported foraging innovations were the cranes and their relatives (Gruidae), falcons (Falconidae), parrots (Psittacidae), hummingbirds (Trochilidae), rails and their relatives (Rallidae), and swifts (Apodidae). Multiple regression showed that incidence of foraging innovations is unrelated to body mass, relative incubation period, mode of development, and life span. How foraging innovation might be related to inherent acceptance or avoidance of new stimuli (neophobia) is an interesting, but unexplored problem (e.g., Marples et al. 1998, Greenberg and

Mettke-Hofmann 2001, Mettke-Hofmann et al. 2002).

The challenge of finding food.—Feeding is a behavior common to all birds, however, different prey present widely different behavioral challenges. I presume that the most challenging types of prey resources are those that exhibit extreme temporal and spatial heterogeneity, such as the prey of most pelagic seabirds, or those that have well-developed abilities to sense and evade predators, such as the prey of many raptorial birds (see also, Clutton-Brock and Harvey 1980, Milton 1988, Dunbar 1992). Other birds handle special challenges, such as those which feed by trapping on changing arrays of flowers (hummingbirds) or widely dispersed fruiting trees (some tropical frugivores). I regarded species that feed on fine-grained food resources, where success is proportional primarily to searching time rather than special searching strategies (foliage gleaners, most seed-eaters, for example), as not requiring well-developed cognitive abilities. I classified foraging as very challenging (2: raptors, swifts, seabirds), moderately challenging (1: corvids, parrots, hummingbirds, plovers, flycatchers, woodpeckers, several tropical fruit-eating groups), and less challenging (0: most opportunistic ground feeders, waterfowl, most passerines).

Analyses of variance with foraging challenge as the main effect were not significant for body mass ($F_{2,32} = 2.82$, $P = 0.075$), but were highly significant for relative brain size ($F_{2,32} = 8.27$, $P = 0.001$, $R^2 = 0.34$) and relative incubation period ($F_{2,29} = 7.06$, $P = 0.003$, $R^2 = 0.33$) (Fig. 4). Relative incubation period increased from foraging class 0 (0.017 ± 0.072 SD, $n = 17$) to class 1 (0.073 ± 0.084 , $n = 11$) and class 2 (0.149 ± 0.071 , $n = 7$); relative brain size increased from foraging class 0 (-0.153 ± 0.141 , $n = 17$) to class 1 (0.062 ± 0.129 , $n = 11$), but was not significantly higher in class 2 (-0.023 ± 0.152 , $n = 7$). Because mode of development is associated with both brain size (precocials smaller) and incubation period (precocials longer), I analyzed the data again only for taxa with altricial development. Precocial species, except plovers, which actively pursue mobile prey, were placed in challenge class 0. In this second analysis without precocial species, relative brain size was no longer significant ($F_{2,18}$

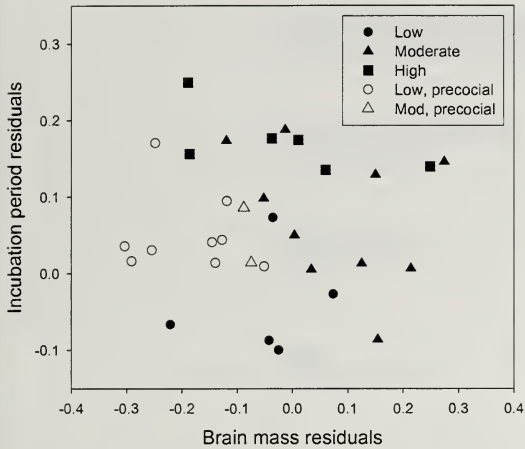


FIG. 4. Groups of birds exhibiting different levels of foraging challenge (circles: low, triangles: moderate, squares: high) as a function of relative brain mass and relative incubation period. Groups with altricial development are shown as filled symbols, those with precocial development as open symbols.

= 1.96, $P = 0.17$), body size was marginally significant ($F_{2,18} = 3.7$, $P = 0.046$, $R^2 = 0.30$), and relative incubation period explained a larger proportion of the variance ($F_{2,18} = 12.7$, $P < 0.001$, $R^2 = 0.60$). Mean relative incubation periods for the foraging classes were (class 0: -0.042 ± 0.070 SD, $n = 5$; class 1: 0.059 ± 0.084 , $n = 9$; class 2: 0.172 ± 0.042 , $n = 6$).

DEMOGRAPHY AND COGNITION

Long life span is strongly associated with a low reproductive rate, delayed maturity, and slow rate of senescence (Ricklefs 1973, 2000; Ricklefs and Scheuerlein 2001). Long life span may also promote the ability of an individual to make use of well-developed cognitive capacities owing to long learning periods, including apprenticeships with older individuals, and extensive experience with temporal and spatial variation in the environment. Most species present evidence of improved reproductive success with experience and age (Coulson 1966, Ollason and Dunnet 1978, Newton 1985, Perrins and McCleery 1985), which may be attributed to the acquisition of information rather than the development of physical skills. Thus, it is reasonable to ask whether species with long life spans demonstrate higher cognitive skills or costs associated with cognition.

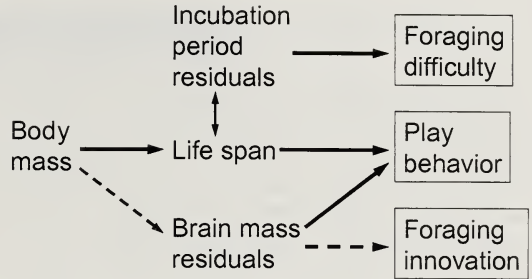


FIG. 5. Connections between life-history variables and indicators of cognitive function revealed by analyses in this study. Dashed arrows indicate weak correlations.

I used as a measure of life span the maximum longevity for a taxonomic group reported in the compilation of Carey and Judge (2000). Among the taxa sampled in this analysis, life span is positively correlated with body mass ($r = 0.43$, $P = 0.017$, $n = 30$), relative incubation period ($r = 0.48$, $P = 0.009$, $n = 29$), and number of publications reporting play behavior ($r = 0.65$, $P = 0.006$, $n = 16$), but not relative brain mass ($r = 0.25$, $P = 0.19$, $n = 30$). Neither the proportion of species exhibiting cooperative breeding ($r = -0.251$, $P = 0.27$, $n = 21$) nor the frequency of reports of innovation ($r = 0.24$, $P = 0.23$, $n = 26$) was significantly related to life span. Life span also did not differ among taxa in different foraging challenge classes ($F_{2,27} = 0.85$, $P = 0.44$). Taxa with higher tendencies to form social groups had marginally longer life spans than less social taxa ($F_{1,28} = 4.5$, $P = 0.042$, $r^2 = 0.14$).

Connections between behavior and life-history variables found in this analysis are diagrammed in Figure 5. Play behavior and foraging innovations are positively related to large brain mass and, in the case of play, long life. Challenges of foraging are more closely associated with relatively long incubation period, which itself is correlated with life span. Thus, several life-history traits might be associated with well-developed cognitive abilities: large brain size, complex brain structure, and slow development as costs (or enabling adaptations); high parental investment, delayed maturity, and long life span as associated traits; and complex foraging and social behaviors as benefits.

DIFFERENT WAYS OF BEING INTELLIGENT

The association of challenging foraging with embryonic development and the association of play and foraging innovation with brain size raises the question of whether there are different ways of being intelligent, each of these relationships representing different components of cognitive ability. Many authors have made the distinction between special and general intelligence, the difference essentially between experience-based decision-making and reasoning (Rozin 1976, McFarland 1989, Vauclair 1996). The first might be thought of as being retrospective, building on the accumulation of information about the environment and processing it in ways to make predictions based on past experience. The ability of seabirds to find their way over thousands of kilometers of ocean and locate quality foraging areas (Jouventin and Weimerskirch 1990, Prince et al. 1992, Weimerskirch and Wilson 2000) may require the accumulation of experience with correlations between weather, oceanographic conditions, and foraging success. If this were true, waiting up to 10 years to achieve sexual maturity (see Ricklefs 1973, 2000) might represent a learning period necessary before an individual can feed even a single chick successfully. Why such a capacity for learning might be related to the length of the embryonic development period rather than brain size is unclear. If this type of information accumulation and processing required an unusually large number of connections per neuron rather than a large number of neurons, the time element might represent the difficulty of making so many connections.

The second kind of cognition might be thought of as prospective, the ability to work out a novel solution to a novel problem, perhaps involving the generation of predictive scenarios based on accumulated experience and detailed observation. However, why this kind of thinking might require a large brain rather than a complex brain is unclear. Nonetheless, the analyses presented here indicate that those birds with relatively higher capacities for reasoning and problem solving, such as corvids and parrots, tend to have large brains.

Do certain preconditions facilitate the evolution of enhanced cognitive abilities?—If certain types of thinking are associated with such life-history traits as large body size, long life span, and prolonged development, the evolution of these traits for other reasons might facilitate the evolution of cognitive ability. Distinguishing preconditions from correlated evolution of traits requires analysis of the distribution of traits on a well-supported phylogenetic hypothesis. Information concerning this issue might also be obtained from the lability of traits within a phylogeny. Conservative traits are more likely to have preceded the evolution of more labile traits owing to their longer histories. However, disparity in the lability of traits also would signal an uncoupling of their evolution. Both relative incubation period and relative brain size are conservative, with most of their variance occurring on the level of families within orders or even higher (Fig. 6). Because we do not have adequate measures of cognitive abilities, it is difficult to determine whether these have a comparable distribution of variance or are more labile. Where groups of birds have been looked at closely with regard to behavior, researchers have tended to emphasize differences between closely related species rather than their similarities or, alternatively, the differences between larger taxonomic groups (Devoogd et al. 1993, Healy and Krebs 1996, Balda et al. 1997, Balda and Kamil 2002). Perhaps differences between closely related species represent the evolutionary elaboration of more generally shared abilities where species are challenged to perform disparate specific tasks.

Consideration of the evolution of cognition leads to another question, namely whether variation in cognition is graded or exhibits thresholds across which abilities change rapidly. This question frequently arises in discussions about the evolution of human intelligence. Some authors suggest that at some point in our evolutionary lineage brain size and intelligent behavior became self-accelerating and our cognitive abilities increased rapidly, creating a substantial gap between humans and other primates in both brain size and intelligent behavior (e.g., Dunbar 1993, Aboitiz and Garcia 1997). Similar thresholds at lower levels of cognitive ability might also lead to the creation of gaps in intelligent be-

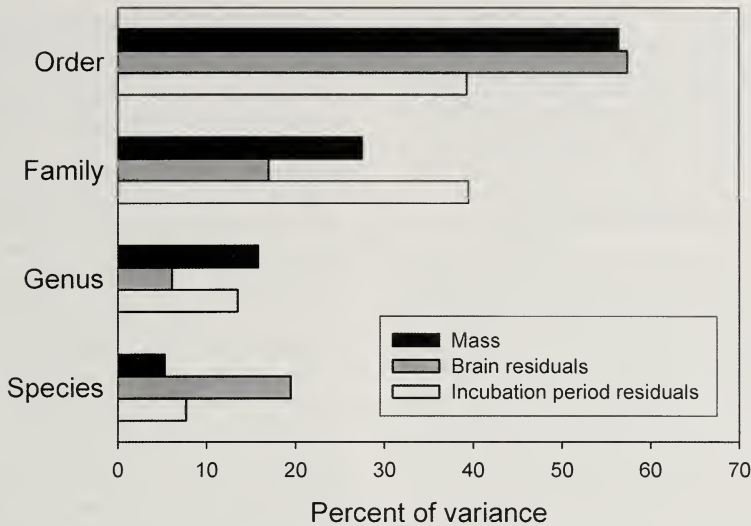


FIG. 6. Distribution of variance components among taxonomic levels for body mass, relative brain size, and incubation period. The relatively high residual for relative brain mass at the species level probably represents, in part, measurement error (i.e., the difficulty of measuring brain mass accurately and the lack of consistency of measurement techniques between studies). For details concerning data and sources, see Ricklefs (1993) and Nealen and Ricklefs (2001).

havior between some species and their close relatives. If the evolution of cognition were similar in different lineages, this might result in well-marked categories of cognitive function across birds, with different lineages having crossed one or more cognitive thresholds. Of course, available data illuminate this issue inadequately, and little more can be said about it at this point, except to remind ourselves how little we know about the evolution of cognition as a life-history trait.

CONCLUSIONS

The ability to act on accumulated experience and the ability to apply reasoning to novel situations are well expressed among birds, although species also differ widely in these abilities. Cognition can be treated as one or, more likely, a set of life-history traits having fitness benefits and costs to the individual. Therefore, it might be possible to judge aspects of cognitive ability indirectly by their associated costs, which plausibly include relative brain size and relative development time. As we understand intelligent behavior better and can place such behavior in a broadly comparative framework, we might develop a more refined definition of the costs of cognition and

improve our ability to recognize cognitive function.

Variation in both relative brain size and relative incubation period resides at a high taxonomic level, suggesting evolutionary conservatism. If these life-history traits are associated with cognition, as argued here, then it is plausible that the evolution of intelligent behavior is also conservative, requiring substantial evolutionary change in structure and development. This contradicts, to some degree, well-documented contrasts between cognitive abilities of some closely related species in particular tests, especially those concerning spatial memory. These different viewpoints might be reconciled if the capacity for intelligent behavior were conservative, but its realization were more labile.

The strongest correlations between putative costs of cognition and intelligent behavior identified in this analysis were associated with play behavior (brain mass) and the challenge of foraging (incubation period). Although the meaning of these statistically significant relationships is obscure, they suggest ways of developing a more broadly comparative appreciation of differences in the behavioral relationships of species to their environments. The

future of this effort to understand cognitive ability as a life-history trait depends on the development of comparative field and experimental studies on many aspects of behavior in birds, combined with a broad assessment of nervous system structure and development.

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EFFECTS OF WEATHER ON PARROT GEOPHAGY IN TAMBOPATA, PERU

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ABSTRACT.—Geophagy is widespread and well documented for mammals, but avian geophagy has only recently become the subject of serious scientific investigation. I analyzed data from 606 mornings of observations at a large avian geophagy site or “clay lick” in the southwestern Amazon Basin to examine the effects of weather on bird lick use. Birds used the clay lick on 94% of the mornings without precipitation or fog. Parrots dominated the site in both numbers of species (17) and individuals (>99%). Weather conditions were significantly correlated with total lick use: there was greater use on sunny mornings and less on rainy mornings. Fog and overnight rain were correlated with low lick use. Sun, rain, fog, and overnight rain were recorded on 47, 25, 20, and 8% of the mornings, respectively. I estimated that inclement weather caused an annual 29% reduction in geophagy for all bird species combined. When early morning rain prevented species from using the lick, they did not return later in the day nor did they compensate for rainy mornings by increasing lick use on subsequent days. The timing of lick use and the lack of compensation suggest that neutralization of toxins could be driving lick use in this system. *Received 25 August 2003, accepted 26 May 2004.*

Geophagy, the intentional consumption of soil, is widespread among vertebrate and invertebrate taxa including mammals, birds, reptiles, and insects (Sokol 1971, Arms et al. 1974, Davies and Baillie 1988, Benkman 1992, Smedley and Eisner 1996). Geophagy occurs on all continents (except Antarctica) and is particularly well documented for mammals, including humans and other primates (Jones and Hanson 1985, Abrahams and Parsons 1996, Klaus and Schmidt 1998, Wiley and Katz 1998, Krishnamani and Mahaney 2000). Recent studies of avian geophagy in tropical areas have focused on soil chemistry, physiology, or short-term observations of behavior (Diamond et al. 1999, Gilardi et al. 1999, Burger and Gochfeld 2003, Brightsmith and Aramburú in press). Long-term studies of geophagy sites are lacking and this hinders our ability to understand the ecological role and relative importance of this phenomenon. Here, I document the effects of weather on avian geophagy in a lowland tropical forest over a 3-year period.

Geophagy is known for members of the avian orders Anseriformes, Columbiformes, Passeriformes, Casuariiformes, Galliformes, and Psittaciformes (Jones and Hanson 1985, Benkman 1992, Wink et al. 1993, Diamond et al. 1999, Keppie and Braun 2000). Of these, the most conspicuous and well studied are the

parrots (Psittaciformes), which gather by the hundreds to consume clay-rich soils from riverbank sites in South America (Emmons and Stark 1979, Gilardi et al. 1999, Burger and Gochfeld 2003, Brightsmith and Aramburú in press). The soils from these “clay licks” apparently provide an important source of sodium and protection against dietary toxins (Diamond et al. 1999, Gilardi et al. 1999, Brightsmith and Aramburú in press). These soils likely permit geophagous species to exploit a wider range of plant resources and allow the high diversity and density of parrots found in the western Amazon basin (Diamond et al. 1999). However, geophagy is not practiced by all psittacids. This variation in geophagous behavior within locations over time and between locations provides an opportunity to explore the ecological role of geophagy.

Weather is known to have strong effects on bird survival and behavior (Silleet et al. 2000, Takagi 2001, Winkler et al. 2002, Cougill and Marsden 2004). Rain and lower temperatures cause short-term increases in nutritional stress for birds and often reduce the frequency of behaviors not critical to immediate survival, including song, migration, communal roosting, and flying (Pyle et al. 1993, Keast 1994, Lengagne and Slater 2002, Lopez-Calleja and Bozinovic 2003, Cougill and Marsden 2004). However, rain and lower temperatures often cause an increase in foraging, a behavior needed for short-term survival (Finney et al. 1999, Fischer and Griffin 2000, Dewasmes et

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al. 2001). I hypothesized that inclement weather (rain and fog) would decrease lick use and that birds would compensate for this decrease by using the lick more after the weather cleared.

METHODS

Study area.—I studied avian geophagy at a clay lick near the Tambopata Research Center (13° 08' S, 69° 37' W) in southeastern Peru. The center is on the border of the Tambopata National Reserve (275,000 ha) and the Bahuaia-Sonene National Park (537,000 ha) in the department of Madre de Dios. The center lies at the boundary between tropical moist and subtropical wet forest at an elevation of 250 m and receives 3,200 mm of rain per year (Tosi 1960; this paper). The research center is located in a small (<1 ha) clearing surrounded by mature floodplain forest, successional floodplain forest, *Mauritia flexuosa* (Arecaceae) palm swamp, and upland forest (Foster et al. 1994). A large patch of bamboo (*Guadua sarcocarpa*; Poaceae) covered the area immediately adjacent to the clay lick, but this patch flowered and died in 2001–2002 (Foster et al. 1994, Griscom and Ashton 2003, DJB pers. obs.). The clay lick is a 500-m long, 25- to 30-m high bank along the western edge of the upper Tambopata River, approximately 300 m from the research center. The cliff is formed by the Tambopata River's erosion of uplifted, Tertiary-age alluvial sediments (Räsänen and Salo 1990, Foster et al. 1994, Räsänen and Linna 1995). The soils of the lick are rich in clay with high cation exchange capacity and high sodium levels (Gilardi et al. 1999, DJB unpubl. data).

Weather data.—From June 1995 through February 2003, researchers at the site recorded weather data. Daily maximum and minimum temperatures were taken from a mercury max-min thermometer located in the understory of primary floodplain forest approximately 20 m from the forest edge. Rain data were collected using a standard rain gauge in a clearing approximately 30 m from the forest edge. Observers recorded the approximate time of rainfall on all days, even when not observing the clay lick. We did not collect weather data every day and gaps of 1 day to >1 month occurred. I calculated mean rainfall for all months in which there were no gaps in

the data >2 days (63 of 93 months). The mean rainfall for each month of each year was used to calculate the overall monthly mean and standard deviation (e.g., the data from January of each year was averaged to provide a composite rainfall for January). Data collected during the El Niño Southern Oscillation of December 1997 to June 1998 were omitted due to the highly irregular patterns of rainfall that typically occur during such events. The average annual rainfall total was calculated by summing the means for each month. Data on the timing and duration, but not intensity of rain, fog, and insolation, were collected during observations of the clay lick (see Bird data below).

Bird data.—Observers recorded bird use at the clay lick on 606 mornings from 12 January 2000 to 16 November 2002. Observers began watching the lick before the birds arrived (approximately at sunrise) until the birds finished their early morning lick use (usually before 07:30 EST). On 280 occasions, observers conducted full-day observations (sunrise until 16:00–17:30), but only early morning data are reported here. Every 5 min, observers recorded the weather as rain (rain falling on the observer), sun (sun hitting the ground anywhere in the vicinity of the clay lick), or cloud (if neither of the others applied). We also noted the presence or absence of fog. Observers recorded the time, number, and species of the first birds that landed on the lick. Starting from this point, observers counted all birds on the lick every 5 min using binoculars and a spotting scope (20–60× zoom). Observers could readily distinguish all of the common bird species on the lick except the two, small, green macaws: Chestnut-fronted Macaw (*Ara severa*) and Red-bellied Macaw (*Orthopsittaca manillata*). For this study, these two species are lumped together and analyzed as “green macaws.”

Data analysis.—I analyzed the correlation between weather variables, month, and lick use using a quasi-likelihood general linear regression (e.g., a Poisson regression with overdispersion; Agresti 2002). This type of model was needed because the birds traveled in flocks and descended to the lick en masse, causing the variance in daily lick use to be greater than the mean. The main effects included in the analysis were year, month,

weather index, rain the night before, fog, daily minimum temperature, daily maximum temperature, lick use the day before, the number of days since the lick was used, and two-way interaction terms. The dependent variable was lick use measured in bird minutes. Bird minutes were defined as the number of birds on the lick multiplied by the number of minutes they stayed on the lick (i.e., 4 birds for 15 min each = 60 bird min). The weather index was a composite variable based on the observations of sun, cloud, and rain recorded every 5 min during observations. It was calculated as the average for each morning with sun = 1, cloud = 2, and rain = 3. Rain the night before was recorded as present if rain fell between 20:00 and 04:00. The variable "fog" used in the model was the sum of the number of 5-min intervals in which fog was recorded during each morning observation. "Lick use the day before" was the number of bird minutes of lick use recorded on the preceding day. The "number of days since the lick was used" was the number of days since birds used the lick. I considered the lick used by birds on a given morning if the total number of bird minutes recorded was >10% of the average for that month. For the calculation of lick use the day before and number of days since the lick was used, I assumed that total lick use was zero for days when heavy rain all morning prevented the observers from going to the lick. This assumption is justified because on 12 mornings, where rain was recorded >80% of the time, total lick use averaged only 39 ± 107 bird min (SD) or 1.3% of the lick use for fair weather days (mean_{fair weather days} = 3051 ± 2465 SD, $n_{fair weather days}$ = 386).

The first regression analysis included all variables. Then I excluded all variables that did not contribute significantly to the model and reran the analysis. Finally, I ran a separate analysis on each of the excluded variables to determine whether any of them contributed significantly to the model (Pyle et al. 1993). The daily maximum temperature was correlated with both the daily minimum temperature (Pearson product-moment correlation = 0.45) and the weather index (Pearson product-moment correlation = -0.35), and it explained less variation than either of the other two, so it was eliminated from the analysis. The interaction coefficient of fog by daily

minimum temperature was highly correlated with the coefficient of fog (Pearson product-moment correlation = 0.998) and the inclusion of the interaction term caused both fog and the interaction to become nonsignificant, so this interaction term was removed from the analysis. This procedure was repeated using lick use for each individual species as the dependent variable. Means are reported \pm SD.

To measure potential lick use, for each month I calculated daily average lick use for each species using data only from "fair weather" mornings (i.e., mornings with no fog, rain, or rain the night before). To measure actual lick use, for each month I calculated daily average lick use for each species using data from all days regardless of weather. For actual lick use, I included mornings with continuous heavy rain when the observers did not go to the lick and assumed that total lick use was zero. The total reduction in lick use due to weather was estimated by the following formula: (potential lick use - actual lick use)/potential lick use.

RESULTS

A total of 28 species of birds ate soil from the lick (Table 1). Parrots dominated the site, both in number of species ($n = 17$) and number of observations (>99%). Thirteen species used the lick regularly in the early mornings (before 07:30) and are included in the analyses presented here. The remaining species were either too uncommon to include in the analysis ($n = 11$) or did not use the lick in the early morning ($n = 4$). Of the 13 species that used the lick in the early morning, 4 also used the lick in the late morning and afternoon (Table 1): Blue-throated Piping-Guan (*Pipile cumanensis*), Blue-and-yellow Macaw (*Ara ararauna*), Scarlet Macaw (*A. macao*), and Red-and-green Macaw (*A. chloroptera*).

Weather.—The average annual rainfall at Tambopata Research Center was 3,236 mm. Monthly mean rainfall ranged from 95 ± 57.7 mm in August ($n = 6$ years) to 528 ± 172.4 mm in January ($n = 7$ years). The months of July and August were the only two in which mean rainfall fell below the estimated potential evapotranspiration (Fig. 1). Rain events of >1 mm were recorded on 42% of the days (709 of 1,679 days). The number of days with rain was greatest in January (mean = $18 \pm$

TABLE 1. Species recorded eating soil from the clay lick at Tambopata Research Center in southeastern Peru, 12 January 2000–16 November 2002. Abundances are given as C (common, seen during $\geq 75\%$ of the observations), U (uncommon, seen $< 75\%$ and $\geq 25\%$), R (rare, seen $< 25\%$ and $\geq 5\%$), or O (occasional, seen during $< 5\%$ of the observations). For species listed as occasional, the number of times seen is reported in parentheses.

	Time of day			Abundance at lick
	Before 07:30	07:30–12:00	After 12:00	
Species analyzed in this paper				
Blue-and-yellow Macaw (<i>Ara ararauna</i>)	x	x	x	C
Scarlet Macaw (<i>Ara macao</i>)	x	x	x	C
Red-and-green Macaw (<i>Ara chloroptera</i>)	x	x	x	C
Chestnut-fronted Macaw (<i>Ara severa</i>)	x			C
Red-bellied Macaw (<i>Orthopsittaca manilata</i>)	x			C
White-bellied Parakeet (<i>Aratinga leucophthalmus</i>)	x			U
Dusky-headed Parakeet (<i>Aratinga weddellii</i>)	x			U
White-bellied Parrot (<i>Pionites leucogaster</i>)	x	x		U
Orange-cheeked Parrot (<i>Pionopsitta barrabandi</i>)	x			U
Blue-headed Parrot (<i>Pionus menstruus</i>)	x			C
Yellow-crowned Parrot (<i>Amazona ochrocephala</i>)	x			U
Mealy Parrot (<i>Amazona farinosa</i>)	x			C
Blue-throated Piping-Guan (<i>Pipile cumanensis</i>)	x	x	x	U
Additional species recorded at the lick				
Speckled Chachalaca (<i>Ortalis guttata</i>)	x	x	x	R
Spix's Guan (<i>Penelope jacquacu</i>)	x	x	x	R
Orange-breasted Falcon (<i>Falco deiroleucus</i>)		x		O (1)
Plumbeous Pigeon (<i>Patagioenas plumbea</i>)		x	x	U
Pale-vented Pigeon (<i>Patagioenas cayennensis</i>)		x	x	U
Ruddy Pigeon (<i>Patagioenas subvinacea</i>)		x	x	U
Blue-headed Macaw (<i>Prinolius couloui</i>)	x			R
Dusky-billed Parrotlet (<i>Forpus sclateri</i>)		x	x	R
Amazonian Parrotlet (<i>Nannopsittaca dachilleae</i>)		x	x	O (9)
Tui Parakeet (<i>Brotogeris sanctithomae</i>)		x	x	O (1)
Cobalt-winged Parakeet (<i>Brotogeris cyanoptera</i>)		x	x	U
Gray-fronted Dove (<i>Leptotila rufaxilla</i>)		x	x	O (2)
Purplish Jay (<i>Cyanocorax cyanomelas</i>)		x	x	O (4)
Blue-gray Tanager (<i>Thraupis episcopus</i>)		x	x	O (4)
Crested Oropendola (<i>Psarocolius decumanus</i>)	x			O (2)

4.1 days, $n = 7$ years) and least in August (mean = 5.5 ± 2.6 days, $n = 6$ years). The mean temperature was $24.3 \pm 1.4^\circ\text{C}$. Early morning fog was recorded on 20% of the days ($n = 606$). Rain was recorded during 12% of the observations ($n = 606$). It rained the previous night during 8% of the observations ($n = 510$); there was no rain or fog of any sort for 76% of the observations ($n = 510$). On 80 days there was heavy rain during the early morning (and observers did not go to the lick on these days).

Weather effects on geophagy.—Birds used the clay lick on 94% of the fair weather mornings (i.e., without rain or fog during the observation or rain the night before, $n = 386$).

The variables month, weather index, fog, and rain the night before explained 47% ($P < 0.001$) of the variation in total lick use (Table 2). As weather progressed from sunny to cloudy to rainy, and fog duration increased, total lick use decreased, explaining 7% of the variation in the data ($P < 0.001$; Table 2). Birds used the lick less on early mornings following rain the previous night ($P < 0.05$; Table 2). Month explained 39% of the variation in total lick use ($P < 0.001$; Table 2); mean daily lick use ranged from $4,784 \pm 2,387$ bird min in August to 257 ± 378 bird min in May (Fig. 2).

When each taxon was analyzed separately, lick use was negatively correlated with weath-

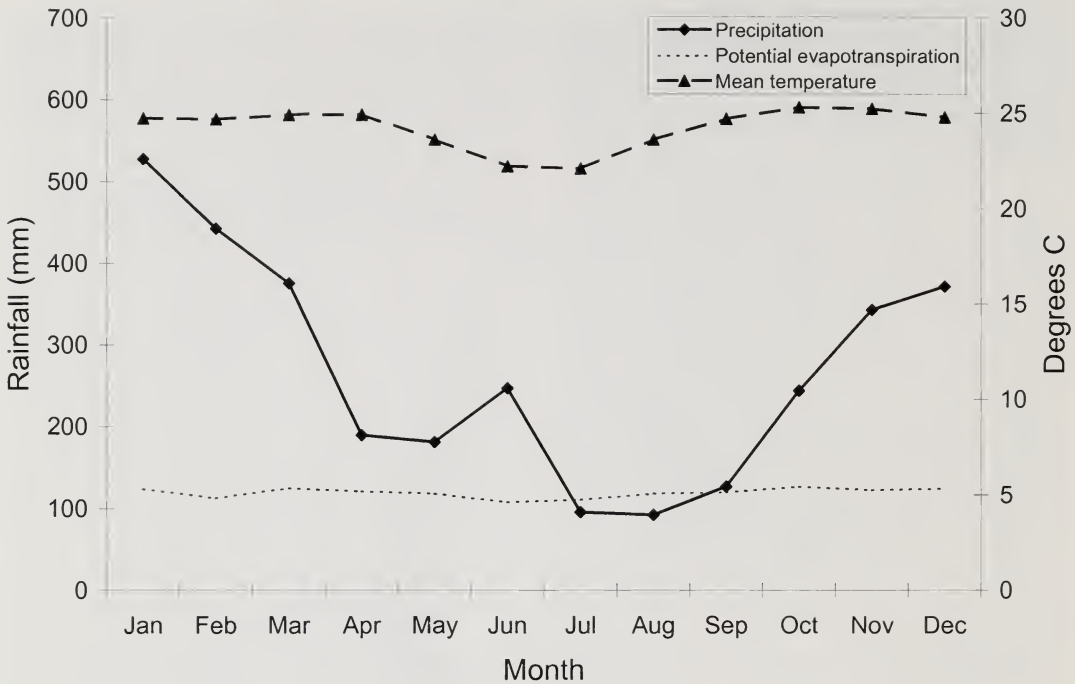


FIG. 1. Mean monthly temperature, rainfall, and estimated evapotranspiration at Tambopata Research Center, Peru, June 1995 through February 2003. Evapotranspiration was estimated following Holdridge (1967).

TABLE 2. Quasi-likelihood general linear regression model (Poisson regression with overdispersion) of weather and month affecting lick use by birds in Tambopata, Peru, 12 January 2000–16 November 2002. Values are presented for combined lick use by 13 species and as the percent deviance explained (regression coefficient). Coefficients with negative values indicate that birds used the lick less as the value of the independent variable increased. A single coefficient cannot be calculated for the categorical variable month, and so is not reported. The model uses the chi-squared-based analysis-of-deviance test. The overall model is significant at $P < 0.001$.

Variable	Deviance (regression coefficient)
Month	39%***a
Weather index	4% (-0.36) ***
Fog	3% (-0.038)***
Rained night before	1% (-0.32)*
Year	NS ^b
Birds yesterday	NS
Days since used ^c	NS
Daily minimum temperature	NS
Month:weather ^d	NS
Month:fog ^d	NS
Daily minimum:weather index ^d	NS
Total df	509
Total deviance	229,190
Deviance explained	47%

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

b NS = not significant ($P > 0.05$).

c Days since used is a measure of how many mornings had elapsed since the lick had been used by birds.

d Variables separated by a colon indicate interactions.

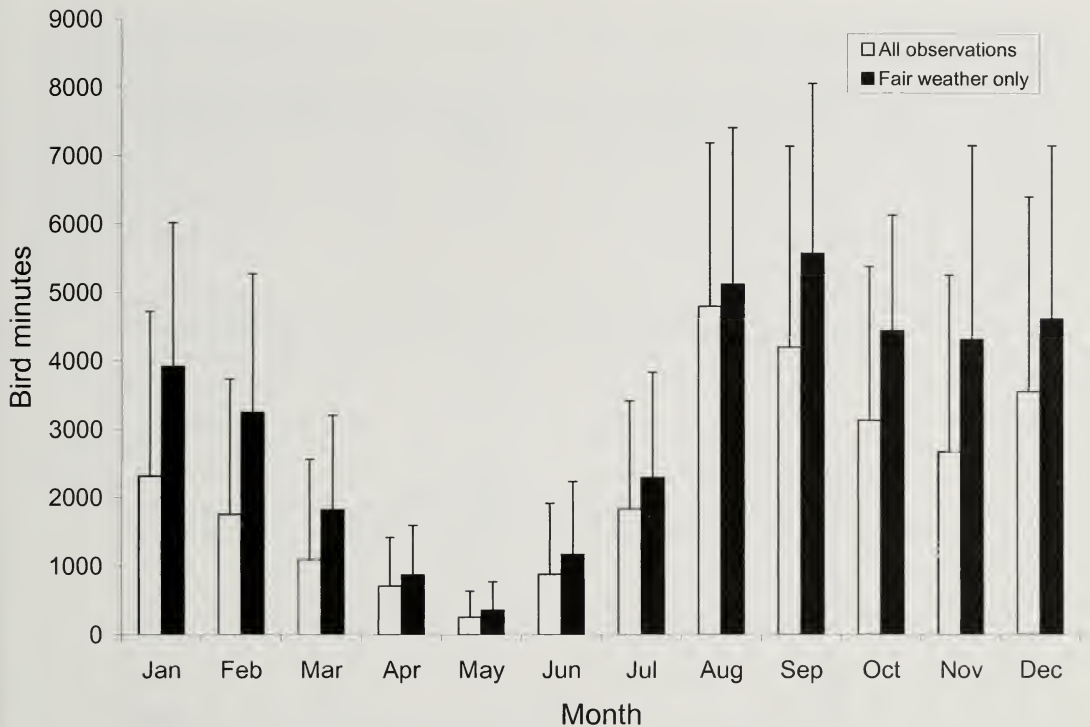


FIG. 2. Mean daily lick use (bird min) by month for all mornings (white bars) and fair weather mornings (black bars) at a clay lick in Tambopata, Peru, 12 January 2000–16 November 2002. Fair weather mornings are defined as those without rain, fog, or rain the night before. Error bars indicate ± 1 SD. The data for fair weather mornings measure potential lick use while data for all days measure actual lick use. The difference between lick use for fair weather mornings and lick use for all mornings is an estimate of the reduction in lick use caused by inclement weather ($n_{\text{fair weather days}} = 307$, $n_{\text{all days}} = 643$).

er index for 7 of 12 taxa analyzed (all $P < 0.05$) indicating that decreased sun and increased rain correlated with reduced lick use (Table 3). Weather index explained 0.4–6.0% of the variation in lick use for these species (Table 3). As fog increased, lick use decreased significantly for 8 of 12 taxa, explaining 0.4–3.0% of the variation in lick use for these species (all $P < 0.05$; Table 3). Four species used the lick less on mornings following overnight rains (all $P < 0.05$; Table 3) while the White-bellied Parrot (*Pionites leucogaster*) used the lick more on mornings following rain ($P < 0.05$). Mealy Parrots (*Amazona farinosa*) showed a positive interaction between weather index and the daily minimum temperature, suggesting that sun and rain had less effect on their lick use during warm days ($P < 0.001$; Table 3). The year-to-year differences were not significant for 8 of 12 species (all $P > 0.05$; Table 3). For the remaining four species

the changes were mixed: Red-and-green and Blue-and-yellow macaws increased with year ($P < 0.001$ and $P < 0.05$, respectively) while Yellow-crowned Parrots (*Amazona ochrocephala*) and White-eyed Parakeets (*Aratinga leucophthalmus*) decreased ($P < 0.05$ both species; Table 3). For Red-and-green Macaw and Orange-cheeked Parrot (*Pionopsitta barabandi*), lick use increased with daily minimum temperature ($P < 0.05$ both species). All species showed a highly significant month effect, indicating strong seasonality in lick use ($P < 0.001$; Table 3). Month explained 17–60% of the variation in the data. For Mealy Parrots, there were significant effects of month by fog and daily minimum temperature by weather index ($P < 0.001$; Table 3).

Lick use on fair weather mornings (a measure of the potential lick use), and lick use on all days, including rainouts (a measure of the actual lick use), showed almost identical

TABLE 3. Quasi-likelihood general linear regression models (Poisson regression with overdispersion) of weather and month on lick use by birds in Tambopata, Peru, 12 January 2000–16 November 2002. Values are presented for 12 taxa representing 13 species that used the clay lick during the early morning (before 07:30). Values are presented as percent deviance explained (regression coefficient). Coefficients with negative values indicate that birds used the lick less as the value of the independent variable increased. Single coefficients cannot be calculated for the categorical variable month or interactions including month, and so are not reported. The model uses the chi-squared-based analysis-of-deviance test. All models are significant at $P < 0.001$.

Variable	Red-and-green Macaw	Blue-and-yellow Macaw	Scarlet Macaw	Green macaws ^f	Mealy Parrot	Yellow-crowned Parrot
Month	23%***	29%***	23%***	17%***	39%***	27%***
Weather index	NS ^b	4% (-0.54)***	6% (-0.60)***	5% (-0.74)***	3% (-5.36)***	NS
Fog	2% (-0.074)**	3% (-0.069)***	3% (-0.056)***	3% (-0.037)***	NS	2% (-0.049)***
Rained night before	NS	1% (-0.60)*	2% (-0.83)**	NS	NS	NS
Year	5% (0.75)***	1% (0.23)*	NS	NS	NS	1% (-0.26)*
Birds yesterday	1% (0.008)*	2% (0.003)**	NS	NS	NS	NS
Days since used ^e	2% (-0.69)**	2% (-0.40)**	NS	NS	NS	NS
Daily minimum temperature	2% (0.17)*	NS	NS	NS	NS	NS
Month:weather index ^d	NS	NS	NS	NS	NS	NS
Month:fog ^d	NS	NS	NS	NS	6%***	NS
Daily min. temp.:weather index ^d	NS	NS	NS	NS	1% (0.21)**	NS
Total df ^e	442	406	509	605	559	605
Total deviance	6,765	21,081	13,579	65,185	145,187	16,140
Deviance explained	35%	42%	32%	25%	48%	30%

Variable	Blue-headed Parrot	Orange-checked Parrot	White-bellied Parrot	White-eyed Parakeet	Dusky-headed Parakeet	Blue-throated Piping-Guan
Month	55%***	59%***	60%***	36%***	27%***	18%***
Weather index	0.4% (-0.14)*	1% (-0.33)**	NS	2% (-0.11)**	NS	NS
Fog	0.4% (-0.022)*	0.5% (-0.030)*	NS	1% (-0.02)**	NS	NS
Rained night before	0.3% (-0.37)*	NS	1% (0.39)*	NS	NS	1% (-1.00)*
Year	NS	NS	NS	6% (-0.26)***	NS	NS
Birds yesterday	NS	NS	1% (0.013)**	11% (0.0018)***	NS	2% (0.037)*
Days since used ^e	NS	NS	1% (-0.40)*	11% (-0.31)*	NS	NS
Daily minimum temperature	NS	1% (0.083)*	NS	NS	NS	NS
Month:weather index ^d	NS	NS	NS	NS	NS	NS
Month:fog ^d	NS	NS	NS	NS	NS	NS
Daily min. temp.:weather index ^d	NS	NS	NS	NS	NS	NS
Total df ^e	509	559	406	477	605	406
Total deviance	120,386	40,211	6,497	67,502	26,217	1,891
Deviance explained	57%	61%	62%	61%	27%	21%

^a $P < 0.05$, ^{**} $P < 0.01$, ^{***} $P < 0.001$.
^b NS = not significant ($P > 0.05$).
^c Days since used is a measure of how many mornings had elapsed since the lick had been used by birds.
^d Variables separated by a colon indicate interactions.
^e Total df vary because different variables had different numbers of observations eliminated due to missing values.
^f The taxon "green macaws" is a combination of Chestnut-fronted and Red-bellied macaws.

month-to-month patterns (Fig. 2). The difference in lick use between fair weather mornings and all mornings combined suggests that inclement weather caused an annual 29% reduction in early morning lick use. Monthly reduction in lick use ranged from 6% in August to 46% in February. Among the 12 taxa analyzed, reduction in lick use ranged from 16 to 37%.

When rain or fog occurred from 05:00 to 07:30 it almost completely prevented the early morning species from using the lick. On 7 of 21 such days, a small number of individuals of the "early morning species" would occasionally use the lick in the late morning or afternoon. However, the number of individuals of early morning species using the lick on these afternoons was always small and total use of the lick averaged <2% of what would have been expected in the early morning (mean = 8.7 ± 6.1 individuals, range 1–19; $\text{mean}_{\text{lick use}} = 87.5 \pm 72.5$ bird min, $n = 7$ afternoons; $\text{mean}_{\text{lick use all mornings}} = 2,540 \pm 2,365$ bird min, $n = 606$ mornings).

Lick use the day before did not show the predicted negative correlation with lick use for all taxa combined (Table 2). When analyzed independently, five taxa showed significant positive correlations between lick use on consecutive days (all $P < 0.05$; Table 3). Similarly, the number of days since the lick was used did not show the predicted positive correlation with lick use (Table 2), and when taxa were analyzed separately, four species showed negative correlations between these variables (all $P < 0.05$; Table 3).

DISCUSSION

Twenty-eight species were seen eating clay at this site, making it the most species-rich avian geophagy site documented (Diamond et al. 1999, Burger and Gochfeld 2003, Brightsmith and Aramburú in press). As with other sites, parrots dominated and pigeons and Galliformes were observed regularly. As hypothesized, inclement weather (morning rain, overnight rain, and morning fog) reduced avian lick use. Lick use varied seasonally but did not vary among years. I did not find the hypothesized increase in lick use following days of low bird use or periods of inclement weather.

of the observations and significantly reduced total lick use. Reasons why birds use the lick less in fog are unknown but could be due to difficulties in navigation, increased chance of collision during flight, or increased probability of predation (Pyle et al. 1993, Bevanger 1994). Parrots using this site come from at least 16 km (DJB unpubl. data) and navigation over such distances could be more difficult or dangerous in foggy conditions. In general, animals approaching geophagy sites are very wary (Izawa 1993, Burger and Gochfeld 2003) presumably due to increased predator densities in the vicinity of geophagy sites (Klaus and Schmid 1998). This wariness is evident at the Tambopata lick and may contribute to the low rate of predation recorded during our work ($n = 4$ confirmed kills in 4,282 hr of observation [DJB unpubl. data], in an area with 34 species of raptors [Rainforest Expeditions 2001]). Birds may be more wary or unwilling to go to the lick during fog if fog reduces their ability to detect approaching predators. The significant interaction between fog and month found for Mealy Parrots suggests that the negative effect of fog varies depending on the month. This could be due to seasonal variation in the density of fog or variation in Mealy Parrots' responses to fog.

Weather index had a strong effect on total lick use. The birds used the lick much less on rainy mornings and more on sunny mornings. While correlations do not prove causality, my observations indicate that birds did not arrive in the area of the lick on rainy mornings, and they frequently abandoned not just the lick itself, but the entire area around the lick as storms approached or as rain began. These observations suggest that rain directly reduced the use of the lick. It is conceivable that the reduction in lick use was due to the birds not wanting to perch on or eat wet soil; the finding that lick use was less on mornings after overnight rain provides some support for this. However, the clays the birds prefer are waterproof due to the high clay and sodium contents (Tan 1996, Gilardi et al. 1999, Brightsmith and Aramburú in press). Water does not penetrate these soils and should have little or no effect on their chemical composition. The finding that lick use on rainy mornings was reduced is consistent with other studies that have shown general reductions in bird activity

Weather effects.—Fog occurred during 20%

during inclement weather (Beintema 1989, Keast 1994, Lengagne and Slater 2002).

Observers in Tambopata have long believed that total lick use is less during the cold weather associated with polar cold snaps or *frijas*. Such cold weather is known to reduce the level of bird activity in warm tropical climates (McClure 1975, Barry and Chorley 1998). My analysis does not support this contention, but it should be noted that the present data set contained only 13 mornings of bird data during *frijas*. Red-and-green Macaws and Orange-cheeked Parrots did show the expected decreased lick use with decreased minimum temperature, suggesting that they may reduce lick use during colder mornings.

When analyzed separately, 9 of 12 species showed reductions in lick use due to inclement weather. Reasons for the variation among taxa are not known and there are no clear inter-specific patterns that suggest an explanation. The parrot species studied here are thought to eat soil for sodium and protection from dietary toxins (Gilardi et al. 1999, Brightsmith and Aramburú in press). Unfortunately, our understanding of the ecological importance of geophagy at this time is insufficient to extrapolate the ecological consequences of this reduction in clay consumption. However, if climate change alters the timing, distribution, or quantity of rainfall, it could have unexpected consequences for these geophagous species.

Seasonal and annual effects.—Geophagy is highly seasonal for nearly all species studied, and the birds at Tambopata are no exception (March and Sadleir 1975, Jones and Hanson 1985, Sanders 1999, Keppie and Braun 2000). For most species, seasonal changes in geophagy are closely linked to diet changes or reproduction (Jones and Hanson 1985, Smedley and Eisner 1996, Sanders 1999). This appears to be the case in Tambopata, as well, where parrots show a sharp increase in lick use during breeding (DJB unpubl. data).

Overall lick use did not vary significantly among years, despite the fact that floods, landslides, and the natural change in the river course have altered the face of the lick during the course of this study. For Red-and-green and Blue-and-yellow macaws, the total amount of lick use in the mornings increased significantly as the study progressed. This is

probably not ecologically significant, as these birds use the lick much more during the late morning and afternoons, outside the time periods considered in these analyses (Burger and Gochfeld 2003, DJB unpubl. data). Yellow-crowned Parrots and White-eyed Parakeets showed significant declines during the course of the study; the reasons for these declines are unknown. There were no significant anthropogenic habitat changes near the study site. Both species are predominantly associated with successional habitats, but the Dusky-headed Parakeet (*Aratinga weddellii*) and Blue-headed Parrots (*Pionus menstruus*) that share these habitats show no similar declines (Forshaw 1989). There are at least two other major clay licks within 50 km of the Tambopata Research Center, and birds moving among these licks could cause the fluctuations. Alternatively, the declines may be part of natural population cycles.

Compensation for lick use lost to inclement weather.—On days when it rained during the early morning (before 07:30), >95% of the members of the nine “early morning” parrot species listed in Table 1 did not eat soil, even if the rest of the day was clear and sunny. Every day there were groups of large macaws that used the lick in the late morning and afternoon (DJB unpubl. data). As a result, large numbers of parrots that were rained out in the morning could have joined these macaw groups and used the lick later in the day. Instead, only a few birds occasionally joined these groups. Effects of weather are strongest on behaviors that are not essential for immediate survival, such as singing, migrating, communal roosting, and flying (Pyle et al. 1993, Keast 1994, Cougill and Marsden 2004). In comparison, either foraging is not as strongly suppressed by inclement weather (Stinson et al. 1987) or lost foraging opportunities are made up through increased effort after the weather clears (Durell et al. 2001). The strong effects of climate and the apparent lack of compensation when birds are denied access to soil suggest that birds do not suffer dire consequences if they are unable to eat soil for a few days, but more detailed studies are needed to test this hypothesis.

To date, there are no data on how often individual birds eat clay. An anecdotal account in Munn (1992) suggests that Red-and-green

Macaws in Manu come to the lick once every 2 to 3 days. If this were the case for the early morning species at Tambopata, I should have found greater lick use on days after the lick was not used, or that lick use was negatively related to lick use the previous day. However, I found that lick use was not correlated with lick use on the previous day. This suggests that the birds make daily decisions to visit the lick based on weather and season and not the amount of time since they have last eaten clay. It also suggests that the birds do not consume more clay to compensate for missed days. For five taxa, the number of birds the day before was positively correlated with lick use, and for four of these taxa the number of days since they had used the lick was negatively associated with lick use. The five species involved (two large macaws, White-bellied Parrot, White-eyed Parakeet, and Blue-throated Piping-Guan) span the range of habitat preference, body size, abundance, group size, seasonality of lick use, and time of day of lick use, making interpretation of this finding difficult.

Reasons for soil consumption.—Previous studies suggest that birds in southeastern Peru consume soil for protection from dietary toxins, sodium deficiency, or both, and the findings of this study may provide some insight (Diamond et al. 1999, Gilardi et al. 1999, Brightsmith and Aramburú in press). The soil protects the birds from toxins by direct adsorption, stimulation of the gut to produce more mucus, and formation of a physical barrier between toxic foods and the gut lining (Gilardi et al. 1999). In addition, sodium and other minerals in the soil may protect the small intestine from tannins (Freeland et al. 1985). The soil stays in the digestive tract for approximately 12 hr; thus, protection from toxins requires daily ingestion of clay before foraging (Gilardi et al. 1999). Because protection from toxins is only effective over the short term, birds should not compensate for days when soil was not consumed. However, the effect of soil on sodium balance is likely to last over more than just 12 hr and birds could make up for missed days through increased consumption on fair weather days. In addition, the timing of clay consumption should be less important if sodium deficiency is driving lick use. As predicted by the pro-

tection from toxins hypothesis, most parrots ate clay first thing in the morning before going off to forage. In addition, birds did not compensate for missed days. These lines of evidence suggest that protection from toxins could be driving lick use. However, evidence from a nearby site suggests that these species choose soil based on its sodium content and not its ability to adsorb dietary toxins (Brightsmith and Aramburú in press). Further insight into lick use would be gained by studies that compare foraging behavior and toxicity of foods eaten on days when birds do and do not have access to clay, and by comparative studies of birds that use the lick in the early morning with those that use the lick later in the day.

The causes and consequences of geophagy are admittedly complex. Detailed physiological and geochemical studies have provided us with insights into the potential benefits of this behavior (Freeland et al. 1985, Jones and Hanson 1985, Gilardi et al. 1999, Mahaney et al. 1999). However, few studies have tied these results directly to the ecology and behavior of species in the wild. This study shows that inclement weather reduces lick use and that birds do not eat more soil to compensate for geophagy opportunities lost to inclement weather. These findings suggest that neutralization of toxins could be driving avian geophagy in this system, but investigators must continue to explore the complex temporal, seasonal, spatial, and taxonomic patterns in soil consumption if we are to determine its true ecological importance.

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USING RADIOTELEMETRY TO MONITOR CARDIAC RESPONSE OF FREE-LIVING TULE GREATER WHITE-FRONTED GEESE (*ANSER ALBIFRONS ELGASI*) TO HUMAN DISTURBANCE

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ABSTRACT.—We monitored the heart rates of free-living Tule Greater White-fronted Geese (*Anser albifrons elgasi*) during human disturbances on their wintering range in the Sacramento Valley of California during 1997. We used implanted radio transmitters to record the heart rates of geese as an observer experimentally approached them at a constant walking speed. On average, geese flushed when observers were 47 m (range: 25–100 m) away. Change point regression was used to identify the point in time when heart rate abruptly increased prior to flushing and when heart rate began to level off in flight after flushing. Heart rates of geese increased as the observer approached them during five of six disturbance trials, from 114.1 ± 6.6 beats/min during the observer's initial approach to 154.8 ± 7.4 beats/min just prior to flushing at the first change point. On average, goose heart rates began to increase most rapidly 5 sec prior to taking flight, and continued to increase rapidly for 4 sec after flushing until reaching flight speed. Heart rate was 456.2 ± 8.4 beats/min at the second change point, which occurred immediately after flushing, and 448.3 ± 9.5 beats/min 1 min later during flight. Although goose heart rates increased as an observer approached, the largest physiological change occurred during a 9-sec period (range: 1.0–15.7 sec) immediately before and after flushing, when heart rates nearly tripled. Received 28 October 2003, accepted 12 April 2004.

Wildlife may incur energetic costs when disturbed by humans; therefore, spatial buffer zones are commonly used by managers to separate wildlife from human activities (Knight and Temple 1995, Camp et al. 1997, Richardson and Miller 1997, Rodgers and Smith 1997). Buffer zones often are based on the distance at which a species flushes in response

to human activities (Richardson and Miller 1997, Rodgers and Smith 1997, Ward et al. 1999, Swarthout and Steidl 2001, Blumstein et al. 2003). However, wildlife may have more subtle physiological responses to disturbances, such as increased heart rate, that also have energetic consequences (MacArthur et al. 1982, Gabrielsen and Smith 1995, Andersen et al. 1996, Weisenberger et al. 1996). Heart rate is a good indicator of an animal's energy expenditure (Wooley and Owen 1977, 1978; Woakes and Butler 1983; Nolet et al. 1992) and depends not only on an animal's physical activity, but also on the level of external stimulation caused by disturbances (Harms et al. 1997, Ely et al. 1999). Therefore, heart rate, rather than flushing distance, may be a better indicator of an animal's stress response to human disturbance (Fernández-Juricic et al. 2001).

In this paper, we provide the first radiotelemetry-based data on the cardiac response of free-living waterfowl to human disturbance. We used implanted radio transmitters to monitor the heart rates of Tule Greater White-fronted Geese (*Anser albifrons elgasi*, hereafter Tule Geese) as an observer experimentally disturbed each radio-marked bird by approaching it at a constant walking speed. We

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report the variation in heart rate throughout the disturbance event from roosting or feeding to flushing and flight, and use change point analysis to identify points in time when heart rate abruptly changed.

METHODS

Tule Geese are larger (>0.5 kg) than the other subspecies of Greater White-fronted Geese (*A. a. frontalis*) wintering in California (Ely and Dzubin 1994). We captured flightless Tule Geese by driving them into net corrals. We implanted radio transmitters in 28 adult female geese on 6 and 8 July 1997 at Kahiltna River Valley, Alaska (see Ely et al. 1999), as part of an aircraft disturbance study of Tule Geese in southcentral Alaska. Thirteen of the 28 transmitters were programmed to be active during 15 days the following winter. To minimize potential confounding effects of capturing and surgically implanting radio transmitters in Tule Geese, we collected heart rate data 5.5 months after the radio-marking procedure when geese were on their wintering grounds in the Sacramento Valley of California. We conducted disturbance trials during the last 2 weeks of December 1997—immediately after closure of the hunting season for dark geese (including Tule Geese)—within the Sacramento and Delevan National Wildlife Refuges and the surrounding agricultural (rice) fields. The main types of human disturbance in this area during our study included waterfowl hunting, farming, vehicular traffic, and birdwatching.

Transmitters (model HRT-150, Telonics Inc., Mesa, Arizona) were covered with a braided surgical mesh (Marlex Mesh, Davol, Charlotte, North Carolina) and implanted into the right abdomen using standard surgical procedures (except that the transmitters had coiled, internal antennas rather than extended, percutaneous antennas; Korschgen et al. 1996). The radio packages could transmit heart rates at a maximum rate of 600 beats/min. Leads of the 44 g transmitter were placed in a base-apex configuration and anchored using 2-vicryl (Ethicon, Somerville, New Jersey). The caudal lead was sutured to the dorsal side of the caudal end of the sternum and the anterior lead was brought through the incision and passed subcutaneously to the left clavicle, where it was sutured just lateral to the sternum. Each transmitter was secured with two

simple, interrupted sutures of 0-vicryl placed through the mesh so that the antenna was situated on the dorsal side of the abdominal cavity, thus increasing transmission range. The incision was closed in two layers using 0-vicryl in a simple continuous pattern. We released the radio-marked geese 2 days after their capture.

We examined the variation in heart rate when Tule Geese were disturbed by approaching a radio-marked goose on foot and simultaneously recording both its heart rate and the time since we initiated the disturbance. During daylight hours, we located radio-marked individuals that were roosting or feeding in refuge ponds or in harvested rice fields that were protected from hunting. After locating a radio-marked goose in a flock, one observer approached on foot (about 0.53 m/sec) while simultaneously recording goose behavior (i.e., on ground, flush, or flying) into a data audio tape recorder (DAT) that added a digital timestamp. At the same time, heart rate signals were being received by a truck-mounted Yagi antenna and ATS receiver (Advanced Telemetry Systems, Isanti, Minnesota), and recorded together with the time on a data logger (Advanced Telemetry Systems, Isanti, Minnesota) that was connected directly to the receiver. We synchronized the observations recorded on the DAT with the heart rate data by documenting precise start times on each recording device. In each trial, the observer continued to approach the radio-marked goose until it flushed, then immediately recorded the precise time of flushing and estimated flushing distance by pacing the distance between the observer and the site where the bird flushed. We continued monitoring heart rates of radio-marked birds in flight for 60 sec after they flushed from the disturbance. We then estimated the starting distance from the observer to the bird by repacing the distance between the site of flushing and the starting point of the observation.

Heart rates recorded on the data logger were transcribed using an ATS DCC II data logger (Advanced Telemetry Systems, Isanti, Minnesota) and a laptop computer with a ProComm macro program developed by ATS, which calculated the radio-marked bird's heart rate every 0.2 sec. We then calculated the average heart rate during each second. For each trial, we used change point analysis (PROC

NLIN, SAS Institute, Inc. 1999; also called segmented regression, Draper and Smith 1998) to fit a three-segment regression and identify the two points in time that flank the period when heart rate changed most rapidly. We examined whether heart rate increased as an observer approached radio-marked geese from the beginning of the trial until the first change point (just before flushing) by testing the slope (m) of this segment of the regression for significant difference from the null hypothesis of no slope (a slope of zero). We calculated the weighted average \pm SE heart rate of radio-marked birds among trials in 5-sec time periods using PROC MEANS (SAS Institute, Inc. 1999). Each measurement was inversely weighted by the sample size for its corresponding time period, so that each trial would have equal total weights of one. We did this for (1) the first 5 sec during our initial approach, (2) the 5 sec immediately before the first change point in heart rate (before flushing), (3) the 5 sec immediately after the second change point in heart rate (after flushing), and (4) during the 55- to 60-sec time period following flushing when the radio-marked goose was in flight. Statistical significance was set at $\alpha = 0.10$.

RESULTS

We successfully documented the cardiac responses of Tule Geese to an approaching observer during six disturbance trials, representing four different birds. Four trials were conducted at Delevan National Wildlife Refuge and two trials were conducted nearby within harvested rice fields. Four additional trials on different birds were excluded due to equipment malfunction (two trials), outside interference by approaching hunters (one trial), or logistical limitations during approach of a radio-marked goose (one trial). The number of radio-marked birds available for study also was limited because we captured and radio-marked Tule Geese 5.5 months before we collected heart rate data in order to minimize any effects of handling and transmitter implantation. By the time radio-marked geese arrived on their wintering grounds, a few radio transmitters had failed and some radio-marked birds could not be located following fall migration.

During five of six trials, heart rates in-

creased from the beginning of the disturbance trial to the first change point as an observer approached the radio-marked goose (Trial 1: $m = 2.54 \pm 0.56$, $t_{82} = 4.54$, $P < 0.001$; Trial 2: $m = 0.28 \pm 0.08$, $t_{175} = 3.51$, $P < 0.001$; Trial 3: $m = 0.10 \pm 0.06$, $t_{204} = 1.77$, $P = 0.08$; Trial 4: $m = -1.50 \pm 1.24$, $t_{76} = -1.21$, $P = 0.23$; Trial 5: $m = 0.40 \pm 0.13$, $t_{170} = 3.07$, $P = 0.003$; Trial 6: $m = 0.56 \pm 0.12$, $t_{160} = 4.65$, $P < 0.001$; Fig. 1). The average distance from observers to radio-marked geese at the start of disturbance trials was 102 m (range: 46–189 m). Heart rates increased from an average of 114.1 ± 6.6 beats/min (range means: 86.6–164.8 beats/min) during the first time period (0–5 sec) when observers began their approach to 154.8 ± 7.4 beats/min (range means: 116.3–199.7 beats/min) during the second time period just prior to flushing at the first change point. Average flushing distance was 47 m (range: 25–100 m). During the third time period, immediately after flushing at the second change point, heart rates averaged 456.2 ± 8.4 beats/min (range means: 417.1–478.0 beats/min); heart rates averaged 448.3 ± 9.5 beats/min (range means: 379.0–518.8 beats/min) during the 55- to 60-sec time period after flushing while in flight. In general, heart rates increased most rapidly at 5 sec (range: 1.2–9.8 sec) prior to flushing and continued increasing rapidly for an additional 4 sec (range: 0.2–8.7 sec) after flushing until reaching flight levels (Fig. 1).

DISCUSSION

The population of Tule Geese is one of the smallest goose populations in North America (about 8,000); the winter range, centered at Delevan National Wildlife Refuge in the Sacramento Valley of California (Callaghan and Green 1993, Ely and Dzubin 1994, Green 1996) is also small. This concentrated wintering distribution potentially subjects the entire population of Tule Geese to negative effects of human disturbance caused by farming, birdwatching, and hunting. In five of six disturbance trials, we found that the heart rates of radio-marked Tule Geese increased as an observer approached them. Heart rates increased by 36% from the time the trial began to the abrupt increase in heart rate that occurred 5 sec before a bird flushed. However, the largest increase in heart rate occurred dur-

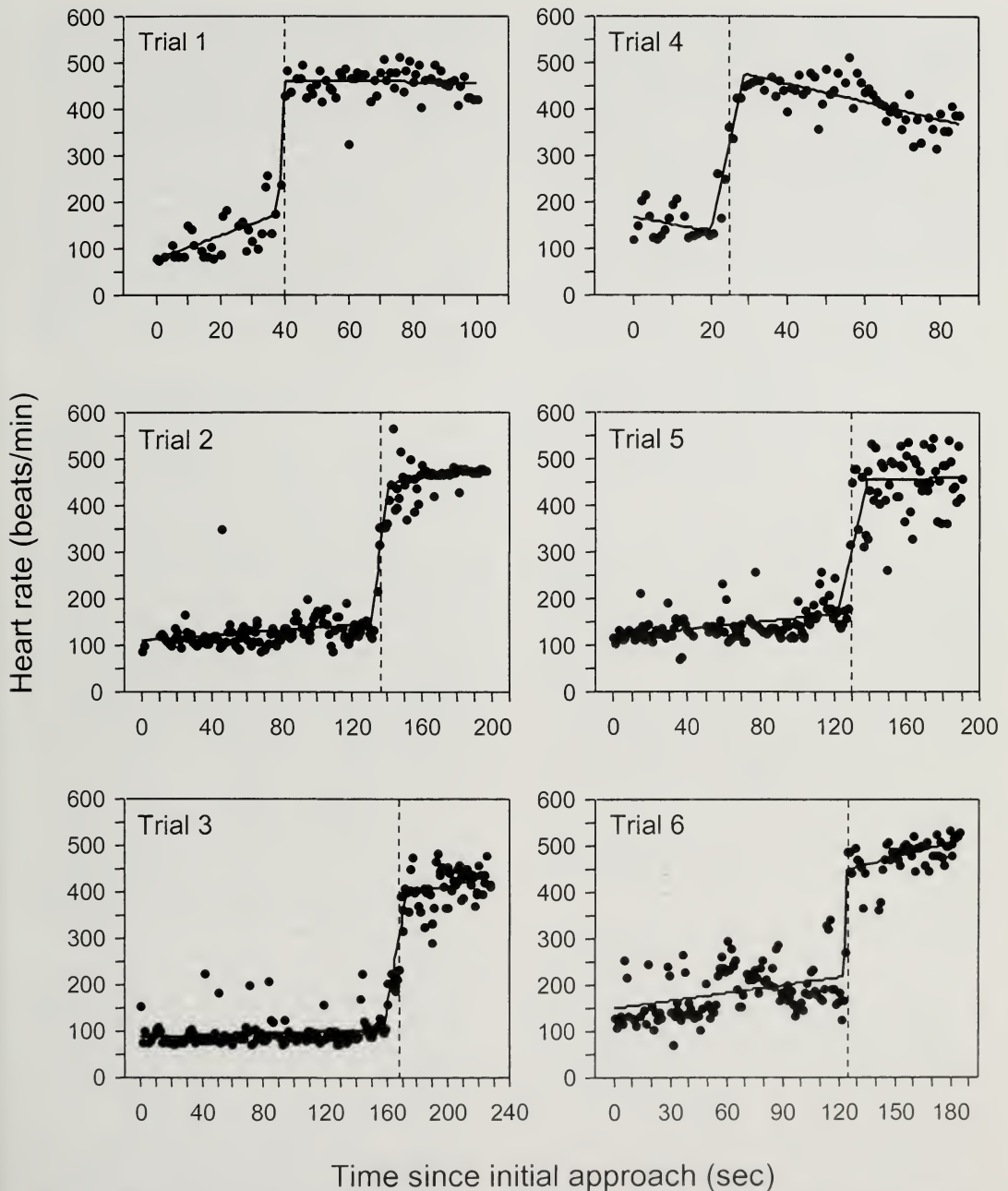


FIG. 1. Heart rates (beats/min) of Tule Greater White-fronted Geese (*Anser albifrons elgasi*) in relation to time elapsed since an observer began approaching radio-marked birds. Each panel represents a single trial conducted in the Sacramento Valley of California, December 1997. Trial numbers one and six, and three and four, were each conducted on the same two individuals, respectively, but on different days. Each data point is the average heart rate of an individual bird during a 1-sec period. The vertical broken lines indicate the time when the radio-marked bird flushed; data to the left of the broken line represent birds on the ground, whereas data to the right of the broken line represent birds in flight. Approximate human-to-bird distances when observers began their approaches for trials 1-6 were 46, 123, 189, 63, 99, and 91 m, respectively. Approximate flushing distances for trials 1-6 were 25, 50, 100, 50, 30, and 25 m, respectively. The solid (mean) lines were fitted using change point analysis.

ing a 9-sec (range: 1.0–15.7 sec) period immediately before and after a bird flushed, when heart rates nearly tripled (Fig. 1). Using our average approach speed of 0.53 m/sec, 5 sec represents only 3 m more than the flushing distance, when their stress response increased appreciably. Therefore, flushing behavior is a reasonable indicator for acute changes in the physiological state of Tule Geese.

Heart rates, however, were slightly elevated for the majority of the time prior to flushing, and self-maintenance activities were disrupted by our disturbance. For example, Tule Geese were alert to our presence and discontinued foraging for the entire duration of our approach. Greater White-fronted Geese (both *A. a. elgasi* and *A. a. frontalis*) typically spend 30% of their time in alert behaviors at foraging sites in the Sacramento Valley during winter (Ely 1992, Hobbs 1999), and heart rates tend to be higher during alert behaviors than when they are walking, feeding, preening, resting, or standing (Ely et al. 1999). If, as we found, alert behavior typically is associated with an elevated heart rate, then alert activity could be energetically expensive, particularly if human disturbances are prolonged prior to flushing. Therefore, alert distance may be a more conservative basis for establishing wildlife buffer zones than flushing distance, especially when disturbances are persistent (Fernández-Juricic et al. 2001, Swarthout and Steidl 2001).

Other studies of disturbance effects on waterfowl have revealed acute changes in heart rate in response to stressful, short-term stimuli. For example, Ely et al. (1999) found that the heart rates of Tule Geese showed the following increases: 80–140 beats/min during non-strenuous activities, 180 beats/min when the birds were alert due to natural stimuli, and >400 beats/min during antagonistic social interactions with conspecifics. Wooley and Owen (1978) observed brief increases in the heart rates of Black Ducks (*Anas rubripes*) in response to approaching herons, hawks, and low-flying planes. Harms et al. (1997) found that heart rates of captive Black Ducks briefly increased in response to simulated aircraft noise. However, in most studies examining the cardiac response of wildlife to stressful stimuli, heart rates quickly returned to normal levels after the stimulus was removed (Kanwish-

er et al. 1978, Wooley and Owen 1978, MacArthur et al. 1982, Weisenberger et al. 1996, Harms et al. 1997, Perry et al. 2002). Therefore, brief disturbances that do not elicit a flushing response by wildlife probably result in minimal energetic costs. We suggest that flushing distance is a reasonable basis for establishing buffer zones when disturbances are likely to be short-term (e.g., automobile or aircraft noise), but that alert distances should be estimated to create buffer zones when disturbances are likely to be long-term (e.g., bird-watchers, hikers).

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DIET OF XANTUS'S MURRELETS IN THE SOUTHERN CALIFORNIA BIGHT

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ABSTRACT.—Most of what is known about diet of Xantus's Murrelets (*Synthliboramphus hypoleucus*) comes from prey found in 19 of 22 murrelet stomachs collected during the 1977 breeding season near Santa Barbara Island in the Southern California Bight (SCB). In May 2002, we examined stomachs of 10 Xantus's Murrelets collected near Anacapa Island, also within the SCB. Seven of the 10 stomachs contained prey. Prey were subadult or adult northern anchovy (*Engraulis mordax*; 2 stomachs), either juvenile bluefin driftfish (*Pseues pellucidus*) or medusafish (*Icichthys lockingtoni*; 2 stomachs), and euphausiids (*Thysanoessa spinifera*; 3 stomachs). Only one prey type was found in each stomach. Our sample added to the diversity of known prey types used in the SCB, including euphausiids and larger age/size classes of fish. We confirmed continued use of northern anchovy, and identified new prey species (bluefin driftfish or medusafish) associated with jellyfish or floating algae and debris in convergence lines. During the breeding season, Xantus's Murrelets appear to be generalist feeders that search for and use available prey that may be concentrated at convergence lines. Received 3 November 2003, accepted 14 June 2004.

In 2004, Xantus's Murrelet (*Synthliboramphus hypoleucus*) was listed by the state of California as a threatened species (Burkett et al. 2003). Knowledge of diet is essential for understanding their foraging ecology, variation in prey resources, at-sea distribution, and at-sea population threats; however, little is known about the diet of Xantus's Murrelet. These birds feed far from shore in small, dispersed groups, usually singles and pairs and occasionally in groups of up to eight birds (Hunt et al. 1979, Briggs et al. 1987, Drost and Lewis 1995, Whitworth et al. 2000). Most dietary information was derived from the examination of stomach contents from 19 of 22 murrelets collected during the 1977 breeding season near Santa Barbara Island, California (Hunt et al. 1979), within the Southern California Bight (SCB). Only larval fish were reported, including northern anchovy (*Engraulis mordax*), Pacific saury (*Cololabis saira*), and rockfish (*Sebastes* sp.). To increase our knowledge of the murrelet's diet, we evaluated non-lethal methods of obtaining dietary information. These techniques failed, and we resorted to using lethal methods to collect 10 murrelets off Anacapa Island in the SCB during April and May 2002. The dietary information that

we obtained may contribute to the conservation of this species.

METHODS

Initially, we evaluated two non-lethal techniques to obtain stomach contents. First, on 20 April 2002 (01:00–02:00 PST), we used a night-lighting technique conducted from an inflatable boat to capture three Xantus's Murrelets from a nocturnal, at-sea congregation near Anacapa Island (Whitworth et al. 1997, 2003; C. D. Hamilton unpubl. data). Captured murrelets were returned to the support vessel, sedated with isoflurane by a veterinarian, and examined with a 2.7 mm endoscope video probe (Karl Storz Veterinary Endoscopy, Goleta, California) that was slowly passed through the mouth, esophagus, proventriculus, and into the gizzard. The digestive tracts of these murrelets were empty, except for traces of unidentifiable green and brown tissue.

Second, we attempted live capture of murrelets during the day with a net gun (Koda Enterprises, Mesa, Arizona) in order to lavage for prey. We searched for murrelets on 13 May (17:30–20:00) and 14 May 2002 (05:00–08:00), but no murrelets were located due to large swells and high winds (Fig. 1). Later on 14 May (08:00), we observed several murrelets near Anacapa Island (Fig. 1). We approached these murrelets at slow speeds in an inflatable boat but determined that they could

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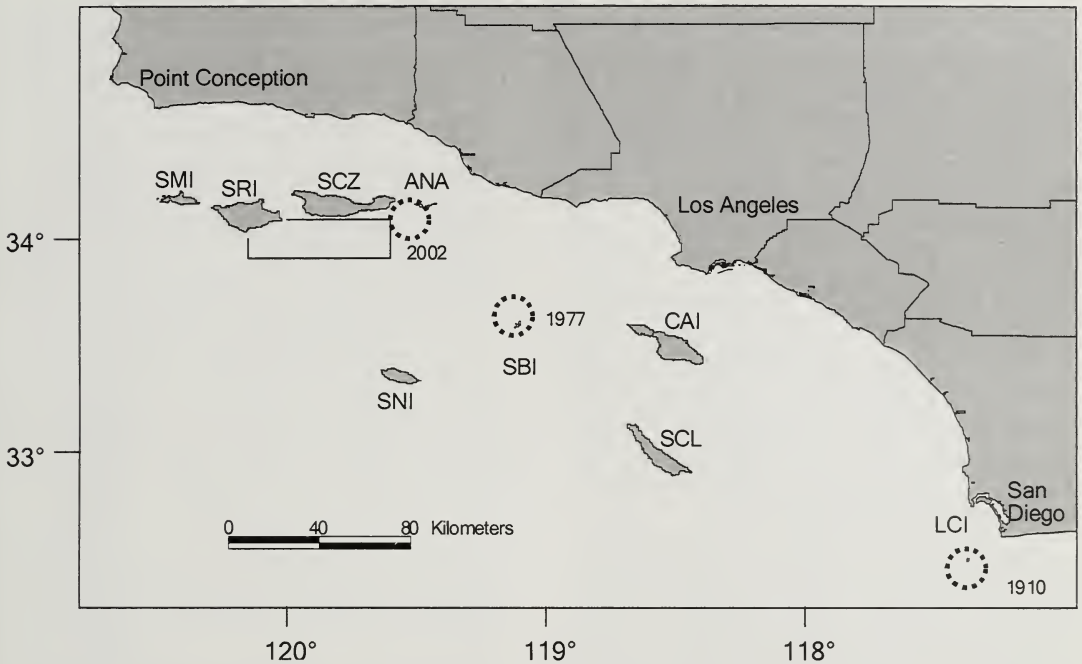


FIG. 1. Xantus's Murrelet collection areas (dashed-line circles) near breeding colonies at Anacapa Island (ANA), Santa Barbara Island (SBI), and Los Coronados Islands (LCI), within the Southern California Bight, California, in 2002, 1977, and 1910, respectively. In 2002, the boxed area was partially searched for capturing murrelets with net guns. Murrelets also breed at Santa Cruz Island (SCZ), San Miguel Island (SMI), Santa Catalina Island (CAI), and San Clemente Island (SCL), but do not breed at Santa Rosa Island (SRI) and San Nicolas Island (SNI) (Carter et al. 1992, Burkett et al. 2003).

not be captured with a net gun: they dove or flushed at distances of 40–50 m and flew less than 0.5 m above the water. For net gun capture, birds need to be within 10–20 m from the gun and fly higher than 0.5 m above the water.

After failing to collect murrelets using non-lethal techniques, we were permitted to collect 10 birds using a shot gun. The collections occurred on 14 May (09:15–11:00; $n = 3$) and 15 May (07:00–08:20; $n = 7$; Fig. 1). We approached murrelets at fast speeds in an inflatable boat, causing them to dive. When they resurfaced after one or more dives, they were shot and carcasses were retrieved immediately.

Within 15–60 min of collection, stomachs were removed and placed in 70% ethanol and bodies were frozen. Stomach contents were sorted and specific identifications were reviewed by individuals experienced with specific prey taxa. Whole and partially digested prey items were counted, total lengths of

whole prey items were measured with calipers, and total lengths of partially digested prey items were estimated from partial measurements (using ratios from morphometric markers). Life stages of prey items were determined from total lengths. Preliminary identifications were checked against descriptions in the literature for lengths, life stages, morphological characteristics, and expected distribution (Baxter 1966, Horn 1973, Kathman et al. 1986, Kucas 1986, Okamoto et al. 2002).

Birds were sexed by gonad inspection. Adults were identified by large testes size, presence of ovarian follicles >1 mm (Nevins and Carter 2003), or presence of brood patches (both sexes incubate). We also gathered morphological data, collected tissues for contaminant analysis, and prepared individuals as museum specimens. Study skins and prey specimens were preserved at the Humboldt State University Wildlife Museum (Arcata, California).

RESULTS

On 14 May 2002 (Fig. 1), we observed 10 murrelets and collected 3. All murrelets were within 100 m of a large, 10-m-wide band of sea foam, floating algae, and other debris that was aligned west-to-east without obvious associated water mixing. On 15 May, we observed an aggregation of 50–100 murrelets and collected 7 more birds (Fig. 1). This aggregation of murrelets was associated with several small, west-to-east convergence lines marked with 1-m-wide bands of sea foam associated with active water mixing at the surface. Based on facial plumage, all 10 murrelets collected belong to the northern subspecies (*S. h. scrippsi*), which breeds primarily in the SCB (Jehl and Bond 1975).

In our sample, 7 of the 10 stomachs contained prey and 3 were empty. Each stomach contained only one prey species (Table 1). Single northern anchovy (subadult or adult) were found in two stomachs collected on separate days. In both cases, the head of each fish had been crushed while the bodies were relatively intact. Two stomachs collected on different days contained either juvenile bluefin driftfish (*Psenes pellicidus*) or juvenile medusafish, (*Icichthys lockingtoni*). Specific identification of these fish was impossible because they were partially digested (i.e., heads entirely disintegrated but tails intact). We narrowed identification to these fish species based on size and morphology of tail and pelvic fins. Tail and pelvic fin morphology are identical for juveniles of these two fish species, and different than that of other species in the SCB. Three stomachs contained mature euphausiids (*Thysanoessa spinifera*).

When collected, 5 of the 10 murrelets were taken from pairs, 4 were in a group, and 1 was alone. Six were adult females and four were adult males. We collected one male-female pair, wherein one stomach contained northern anchovy and the other was empty. The group of four murrelets collected together may have represented two pairs (i.e., two males and two females); three of these had fed on euphausiids while the other had an empty stomach. One of these females had recently laid at least one egg (based on the presence of a post-ovulatory follicle, enlarged oviduct, and developing brood patches), and the asso-

TABLE 1. Comparison of diet of Xantus's Murrelets collected near Santa Barbara Island, California, in 1977 (Hunt et al. 1979) and near Anacapa Island, California, in 2002 (this study).

Prey items (species)	1977 collections			2002 collections					
	Life stage	% Occ ^a	n ^b	Life stage	% Occ ^a	n ^b	Mean ^c	Range ^c	Range of length (mm)
Euphausiid (<i>Thysanoessa spinifera</i>)	—	—	0	Mature	43	3	8.3	5–12	25–30
Northern anchovy (<i>Engraulis mordax</i>)	Larval	42	8	Subadult/adult	29	2	1	1	95–110
Medusafish (<i>Icichthys lockingtoni</i>) or bluefin driftfish (<i>Psenes pellicidus</i>)	—	—	0	Juvenile	29	2	2.5	1–4	35–40
Pacific saury (<i>Cololabis saira</i>)	Larval	11	2	—	—	0	—	—	—
Rockfish (<i>Sebastes</i> sp.)	Larval	11	2	—	—	0	—	—	—
Unidentified fish	Larval	37	7	—	—	0	—	—	—
Empty	—	—	3	—	—	3	—	—	—

^a % Occ = (number of stomachs with specific prey type/number of total stomachs with prey) × 100. Data from Hunt et al. (1979) were recalculated using this method.

^b Sample size is number of stomachs containing each prey item. For the 1977 collections, sample size was calculated using percent occurrence reported in Hunt et al. (1979), and 22 total stomachs collected.

^c Items/stomach.

ciated male had developed brood patches. None of the other murrelets had brood patches or exhibited signs of egg laying.

DISCUSSION

Until 1977, little was known about the diet of the Xantus's Murrelet. Howell (1910:185) reported that Xantus's Murrelets collected during May to July 1910 at Los Coronados Islands, Mexico (Fig. 1), "feed upon all kinds of small sea life, including crustaceans . . . [some] contain a certain green sea-weed. . . ." Dawson (1923) reported that they fed on "marine invertebrates," but no details were provided. Miller (1936) reported that one murrelet collected during July or August 1935 off San Diego contained "several small fish." One dead murrelet collected on the beach in Douglas County, Oregon, in February 1989 contained sandlance otoliths (*Ammodytes* sp.; Los Angeles County Museum #105851, collection notes).

In 1977, 19 of 22 stomachs from birds collected offshore of Santa Barbara Island contained prey, and each stomach apparently contained only one prey type (based on our calculations from percent occurrence reported in Hunt et al. 1979). Eight stomachs (42% of stomachs with prey) contained larval northern anchovies and 11 contained other fish species (Table 1).

Our 2002 sample added to the diversity of prey types and age/size classes of fish known to be utilized by Xantus's Murrelets. Anchovies—all subadults or adults—were present in 29% of stomachs. In the 1977 sample, all anchovies found in murrelet stomachs were larval. Use of euphausiids was first documented in 2002, although unidentified marine invertebrates were noted in the historical literature. *Thysanoessa* euphausiids are common prey for Cassin's Auklets (*Ptychoramphus aleuticus*) during the breeding season in the northern SCB (Hunt et al. 1979, Adams 2004) and for Marbled Murrelets (*Brachyramphus marmoratus*) during the non-breeding season in Alaska (Sanger 1987). Neither bluefin driftfish nor medusafish have been reported previously as prey species for Xantus's Murrelets. Medusafish are uncommon alcid prey but have been reported to be taken by Tufted Puffins (*Fratercula cirrhata*; Baltz and Morejohn 1977). Bluefin driftfish have not been reported

previously as alcid prey. The juvenile stages of both species are associated with jellyfish and floating weed patches (Horn 1973, Okamoto et al. 2002). Their presence in murrelet diet likely reflected murrelets foraging near convergences of floating patches of debris, algae, and sea foam. These juvenile fish were much smaller than the subadult or adult anchovies found in 2002.

Radio-marked Xantus's Murrelets from Santa Barbara Island in 1996–1997 (Whitworth et al. 2000) and Anacapa Island in 2002–2003 (C. D. Hamilton unpubl. data) were reported using Anacapa Passage (between Anacapa and Santa Cruz islands; Fig. 1) in the same area where we collected murrelets. Thus, the collected murrelets could have been from several SCB breeding colonies, and Anacapa Passage may be an important foraging area for Xantus's Murrelets. The collected murrelets contained different fish and euphausiid prey species, indicating that several prey types were available in that area in mid-May 2002. Only one prey type, however, was found in each stomach in 2002 and 1977, indicating that feeding occurred on one prey type at a time. Three of four murrelets collected together were feeding on euphausiids, indicating that murrelets found together may be exploiting the same prey resources.

Synthliboramphus murrelets dive for and feed on a variety of small fish and zooplankton and are considered to be generalist feeders (Sealy 1975, DeWeese and Anderson 1976, Gaston 1992, Gaston et al. 1993, Gaston and Jones 1998). Dietary information from 1977 and 2002 breeding seasons indicated that while Xantus's Murrelets feed on a variety of prey types, northern anchovy may be the most common prey in the SCB during the breeding season. Little is known about diet during the non-breeding season (murrelets disperse as far north as British Columbia, Canada) or about diet of the southern subspecies (*S. h. hypoleucus*), which breeds off the central west coast of Baja California, Mexico.

A cool-water period from 1950–1975 had made conditions favorable for anchovy abundance in the SCB (Chavez et al. 2003), and could have led to frequent consumption of anchovies (42% occurrence) in 1977. In 1978, when the availability of larval anchovies was delayed (Lasker 1979), murrelets exhibited

delayed breeding or failed to breed. This suggests that larval anchovy abundance affected reproductive success and survival of murrelets (Hunt and Butler 1980). Larval anchovies, however, were not found in the 2002 sample; thus, overall prey abundance and availability may be more important factors influencing reproductive success and survival. Large-scale variations in water temperature that occur in the SCB are known to affect the abundance of anchovies, zooplankton, and other fish species (Roemmich and McGowan 1995, Chavez et al. 2003, Lluch-Belda et al. 2003), and these variations likely affect Xantus's Murrelets during the breeding season.

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RADIO-TAGGED PACIFIC GOLDEN-PLOVERS: FURTHER INSIGHT CONCERNING THE HAWAII-ALASKA MIGRATORY LINK

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ABSTRACT.—We radio-tagged 55 Pacific Golden-Plovers (*Pluvialis fulva*) in spring 2001–2003 on wintering grounds in Hawaii. Following their northward migration (most birds deserted winter territories in late April), we relocated 15 golden-plovers in three regions of Alaska: Copper River Delta, King Salmon, and Kotzebue. One individual made the transpacific flight from Oahu to the Alaska Peninsula in a minimum time of 70 hr at a minimum flight speed of 56 km/hr. Our findings, together with earlier records, indicate a major Hawaii-Alaska migratory connection for this species, and suggest that plovers wintering on Oahu nest throughout the known Alaska breeding range. Post-breeding, 84% of the sample birds returned to Oahu and reoccupied their previous winter territories. Received 21 November 2003, accepted 10 June 2004.

The first investigations of radio-tagged Pacific Golden-Plovers (*Pluvialis fulva*) on the mid-Pacific flyway were conducted in 1996 and 1999. In these studies, birds from wintering populations on Oahu, Hawaii, were found after transoceanic spring migration at three locations in Alaska (Johnson et al. 1997, 2001a). While migrating northward, one of the plovers spent time at the Copper River Delta stopover and then proceeded on to breeding grounds in the Nushagak River drainage northwest of Lake Iliamna; others were detected (presumably nesting) in the Nushagak River area and on the Yukon-Kuskokwim Delta. Here, we present additional telemetry findings that further clarify spring movements and destinations of plovers in Alaska. We also report the post-breeding return rates to wintering territories in Hawaii.

METHODS

Over three spring seasons, we captured 55 plovers on Oahu—20 each in 2001 and 2002, and 15 in 2003. The birds (24 adult males, 22 adult females, 3 first-year males, and 6 first-year females) were caught mostly during the third week of April with mist nets on lawn areas at three wintering ground study sites: National Memorial Cemetery of the Pacific, Hickam Air Force Base, and Bellows Air Force Station. These are the same sites where plovers were radio-tagged in previous investigations (Johnson et al. 1997, 2001a). We uniquely color-banded each plover and glued a 1.65 g, 60-day life span transmitter (Holohil Systems, Carp, Ontario) to feather stubs on the lower back (see Warnock and Warnock 1993). Such attachment was temporary, as radios would be expected to fall off during summertime prebasic molting on the tundra (Johnson and Connors 1996). Based on the weights of birds closest to migratory departure (mean = 173 g, range = 148–207 g, $n = 18$; all captured on either 19 or 20 April, about 1 week pre-migration) plus comparable data from the same sites in other years (Johnson et al. 1997, 2001a; OWJ unpubl. data), the attached transmitters generally averaged less than 1% of total mass at migration. For additional information on capture, marking, and determination of sex and age, see Johnson et al. (1997, 2001a, 2001b).

All of the radio-tagged plovers defended specific winter territories on lawns at the study sites; thus, we could monitor them easily after

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FIG. 1. Detections of radio-tagged Pacific Golden-Plovers (*Pluvialis fulva*) in Alaska. Numbers in circles represent the present study (2001–2003), numbers in squares show previous findings (Johnson et al. 1997, 2001a). Over all years, we recorded 32 detections of 28 birds. Four individuals made long-range movements following first detection (see text). Darker gray shading shows the approximate nesting range of *P. fulva* in Alaska. Abbreviations: CRD (Copper River Delta), Anc (Anchorage), KS (King Salmon), Nu (Nushagak River drainage), Be (Bethel), Ko (Kotzebue).

release. We checked for the presence of tagged birds several times a day (with a radio receiver and/or visually), and considered disappearance from a territory as an indicator of migration (Johnson et al. 1997, 2001a, 2001b). This plover is strongly site-faithful to winter territories from one season to the next (Johnson and Connors 1996, Johnson et al. 1997, 2001a, 2001b), which enabled determination of return rates in the fall.

In Alaska, we monitored radio frequencies in the Copper River Delta, King Salmon, and Kotzebue regions (Fig. 1) using fixed-wing aircraft equipped with VHF receiving antennae. Aerial surveys were conducted from late April to the third week of May at the Copper River Delta and King Salmon areas, and from mid-May to mid-June at Kotzebue. Surveys were typically coincident with other telemetry

projects involving the same aircraft. The areas traversed by monitoring flights were approximately as follows: Copper River Delta—coastal flats from Cordova to Controller Bay; King Salmon—Dillingham to Inlik, coastline to 10 km inland; Kotzebue—Kivalina to Deering, coastline to 30–50 km inland. There were 2–3 flights per season in the Kotzebue region. Monitoring efforts were more variable in the other areas: Copper River Delta—19 flights in 2001, 6 in 2002, 1 in 2003; King Salmon—11 flights in 2001, 7 in 2002, 2 in 2003. With the exception of the Copper River Delta, we recorded GPS coordinates whenever a radio-tagged plover was detected.

RESULTS

During the 2001–2003 spring seasons, migratory departure (as indicated by disappear-

ance of birds from their winter territories) occurred from 17 April to 9 May, with almost all departures taking place in late April. Collectively, 44 of the 55 plovers (80%) departed from 22 to 29 April, 3 birds (5%) disappeared before 22 April, and 8 (15%) after 29 April. Much the same pattern (OWJ unpubl. data) was observed in our 1996 and 1999 studies, when 56 of 60 birds (93%) disappeared from 23 to 29 April, 1 bird (2%) before 23 April, and 3 birds (5%) after 29 April. Based on combined records from all plovers we have radio-tagged (65 males and 50 females in 1996, 1999, and 2001–2003), earlier departures were somewhat male-biased. Over all years, 97% of males and 82% of females had left their territories by 29 April; the last birds at our study sites each spring were typically females. There was no indication that radio-tagging delayed departures, as tagged and untagged birds deserted their territories at similar rates, and generally the last few individuals to leave were untagged. More females (10) than males (5) were relocated in Alaska from 2001 to 2003, but there was no statistical difference between the sexes ($\chi^2 = 0.13$, $df = 1$, $P = 0.72$) when relocations in previous studies (Johnson et al. 1997, 2001a) were combined with the present sample. Over all years, 15 of 65 males and 13 of 50 females radio-tagged on Oahu were relocated in Alaska (Fig. 1).

The number of birds detected varied among years: nine in 2001, five in 2002, and one in 2003. Inter-year variation apparently resulted from the number of flights per season, survey timing (either too early or too late), lack of plover-specific monitoring (i.e., coverage was probably compromised by coincident monitoring of frequencies from other telemetry projects), and weather factors that reduced the duration and/or effectiveness of some flights.

We relocated two plovers (CRD 1 and CRD 2) at the Copper River Delta in 2001. From this stopover, situated well to the east of the nesting range, each bird moved westward and was detected again—CRD 1 to the south of Kotzebue, and CRD 2 to the south of King Salmon. Assuming straight-line distances, these flights were about 1,100 and 750 km, respectively. Ten plovers (including CRD 2) were found along the western edge of the Alaska Peninsula and west of King Salmon (Fig. 1). One set a record of 70 hr elapsed time

between our last contact with the bird on Oahu and its relocation in Alaska. Following its detection south of King Salmon, this bird then moved northward to breeding grounds near Kotzebue. In the Kotzebue survey area, we found six radio-tagged plovers, including the aforementioned 70-hr individual and CRD 1.

Eighty-four percent of the sample population (46 of 55 birds) returned to Oahu during the first fall after banding and each bird re-occupied its previous winter territory. The return rate did not differ significantly ($\chi^2 = 0.33$, $df = 1$, $P = 0.56$) from that of plovers that were banded, but not radio-tagged, at the same study sites (144 of 166, 87%; Johnson et al. 2001a). Of the nine individuals that failed to return, five were females and four were males. Based on all plovers we have radio-tagged (Johnson et al. 1997, 2001a; plus the present sample), there was no difference between the sexes among birds that did not return (10 of 65 males versus 8 of 50 females; $\chi^2 = 0.01$, $df = 1$, $P = 0.93$).

DISCUSSION

Relocation of two radio-tagged birds at the Copper River Delta from late April to early May 2001, and another individual in 1996 (Johnson et al. 1997), indicates that some Pacific Golden-Plovers migrating from Hawaii use the delta region as a refueling site. Whether this is an intended landfall or a deflection caused by prevailing winds during transoceanic passage is uncertain. Repeated contacts with the radio-tagged plovers at the delta suggested that their stays there lasted about 1 week. Following this stopover, both of the 2001 birds moved westward and each was detected again in tundra habitat where they may have been nesting (Fig. 1). The 1996 bird made a similar movement from the delta to the Nushagak River region, where it was detected in late May (Johnson et al. 1997).

Detection of 12 radio-tagged plovers in the King Salmon region (10 from the present study; 2 previously, Johnson et al. 1997, 2001a) from Port Heiden to the mouth of the Kvichak River (between 57° and 59° N) suggests that this part of the Alaska Peninsula is an important spring destination for birds wintering on Oahu. Some birds stopping here are en route to areas much farther north (as shown by one radio-tagged plover subsequently re-

located near Kotzebue); others may be in passage to less distant breeding grounds, such as the Nushagak River drainage (Fig. 1; Bennett 1996, Johnson et al. 2001a). It is also possible that some of the birds detected on the Alaska Peninsula are nesting there. During a 15 May–5 June 2002 shorebird survey at various sites on the peninsula, C. Wightman (in litt. 2002) “recorded Pacific Golden-Plovers performing display flights to approximately 57 degrees 30 minutes latitude,” essentially the same latitude where we received signals from several of our radio-tagged birds. The timing of Wightman’s observations strongly suggests that they represented breeding birds, but as yet no intensive nest searches have been conducted. If nesting is confirmed at that latitude, it would extend the breeding range at least 250 km farther south than currently recognized (Fig. 1; also see Johnson et al. 2001a).

The minimum flight time of 70 hr from Oahu to near Port Heiden on the Alaska Peninsula is the shortest interval thus far recorded (previously 90 hr, see Johnson et al. 1997) for the transpacific passage. Assuming a great circle route of approximately 3,900 km, this bird’s minimum flight speed was 56 km/hr. Given the high-speed flight characteristic of the species (Paulson 1993, Johnson and Connors 1996), the actual flight time was probably less and the speed greater than we recorded. Measurements of flight-time and speed are complicated by a number of difficult-to-resolve variables, including time spent in pre-departure staging, routes followed, and the interval between arrival and detection in Alaska.

The relatively high rates of fall returns confirmed earlier conclusions (Johnson et al. 1997, 2001a) that radio-tagging caused no apparent harm to the birds. While this is reassuring, it remains uncertain whether transmitters interfere in any way with the reproductive process. Both sexes returned at equal rates and this further substantiated past findings (in part from birds not radio-tagged) of no sex-related bias in mortality during the migration or breeding periods (Johnson et al. 1993, 2001a, 2001b; OWJ unpubl. data).

Our aerial surveys in Alaska covered a relatively small fraction (probably <10%) of the area in which Pacific Golden-Plovers either nest or likely stop to refuel. Nonetheless, we relocated 15 of 55 (27%) from 2001 through

2003 and 13 of 60 (22%) in previous years. Our findings suggest that a substantial portion of the birds wintering on Oahu breed in Alaska. Whether some fraction of Oahu birds breeds in eastern Siberia is unknown. Our data also suggest that plovers wintering on Oahu nest throughout the known breeding range in Alaska (Fig. 1). Similar linkages seem likely for plovers wintering elsewhere in Hawaii, but proof will require additional radio-tagging in other parts of the archipelago.

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BEHAVIORAL INTERACTIONS BETWEEN FIRE ANTS AND VERTEBRATE NEST PREDATORS AT TWO BLACK-CAPPED VIREO NESTS

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ABSTRACT.—We report on behavioral interactions between fire ants (*Solenopsis invicta*) and vertebrate predators at two Black-capped Vireo (*Vireo atricapilla*) nests at Fort Hood, Texas. In the presence of fire ants, an eastern woodrat (*Neotoma floridana*) failed to depredate a clutch of vireo eggs at one nest, while a rat snake (*Elaphe obsoleta lindheimeri*) depredated nestlings at another nest, despite fire ants swarming the nest. Neither nest was successful. Direct and indirect effects of interactions among nest predators on avian nesting success need further assessment. Received 21 November 2003, accepted 7 June 2004.

The red imported fire ant (*Solenopsis invicta*) is an invasive species that occurs throughout much of the southern United States (Porter et al. 1991, Callcott and Collins 1996, O'Keefe et al. 2000), where it poses a serious threat to terrestrial communities (Wojcik et al. 2001, Holway et al. 2002). It preys upon birds (Sikes and Arnold 1986, Allen et al. 1995, Kopachena et al. 2000), small mammals (Killion et al. 1995, Ferris et al. 1998), and reptilian eggs and hatchlings (Mount et al. 1981, Buhlmann and Coffman 2001, Parris et al. 2002). Fire ants may reduce population densities of small mammals (Killion et al. 1995, Ferris et al. 1998) and cause shifts in small mammal foraging patterns (Holtcamp et al. 1997). Tuberville et al. (2000) suggest that fire ants also may influence snake populations, but there is no evidence that they depredate adult snakes. Fire ants appear to out-compete native ants and arthropods for invertebrate prey (Apperson and Powell 1984, Morrison 2002). Competition between fire ants and other pred-

ators for vertebrate prey, however, has not been documented except in the recent case where fire ants consumed shrike-cached food (Allen et al. 2001). Here, we document the behavioral interactions between fire ants and two vertebrate nest predators, an eastern woodrat (*Neotoma floridana*) and a Texas rat snake (*Elaphe obsoleta lindheimeri*), at two nests of the Black-capped Vireo (*Vireo atricapilla*).

METHODS

Predator activity was recorded as part of ongoing monitoring and management of Black-capped Vireos at Fort Hood, an 88,500-ha military installation in Bell and Coryell counties, Texas (30° 10' N, 97° 45' W). Twelve infrared video systems (Fuhrman Diversified, Inc., Seabrook, Texas) were deployed to monitor 142 nests for 1,589 exposure days (773 in the incubation stage and 816 in the nestling stage) from 1 April to 31 July, 1998–2001. A detailed description of the video-monitoring protocol is given in Stake and Cimprich (2003). We quantified predation events and predator interactions when fire ants were at vireo nests. Vireo behavior was categorized as aerial defense when birds were observed in the video monitor at least once within a 20-sec interval and perched on the focal nest for no longer than 2 sec. During aerial defense, vireos actively pecked at and removed fire ants swarming the nest.

Ants from vireo nests were identified in the field as fire ants (by MMS) during daily maintenance of video cameras. In a separate study, SJT (unpubl. data) collected ant samples

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across Fort Hood at 135 points on a 2,000-m grid, and also conducted bi-monthly ant sampling for one year at 150 bait trap stations in vireo nesting habitat. This vouchered material was identified in the laboratory, and the only *Solenopsis* species in these samples was *S. invicta*. On rare occasions the native fire ant, *S. geminata*, has been collected at bait stations in other studies at Fort Hood (C. E. Pekins pers. comm.), leaving open the remote possibility that the ants observed in our study could have been native fire ants.

RESULTS

Of 134 vireo nests, 48 (35.8%) failed due to direct predation, where predators removed or damaged some or all of the nest contents (Stake and Cimprich 2003). Fire ants were among these predators and they directly depredated 15 nests (31.3%). Abandonment by vireos in response to fire ants was the source of failure at six additional nests. Thus, fire ants caused failure at 21 nests (29.6%) when direct predation and abandonment were combined.

All depredated nests, except three, were attacked by a single predator. In the first nest, a Brown-headed Cowbird (*Molothrus ater*) removed one nestling, and 2 days later a snake consumed the remaining nestlings. At the second nest, an eastern woodrat failed to depredate a clutch of vireo eggs in the presence of swarming fire ants. At the third nest, a rat snake depredated vireo nestlings in the presence of fire ants. Interactions of predators at the second and third nest are discussed below. Based on careful examination of the video tapes, we estimate that hundreds of fire ants swarmed each of these nests.

On 15 June 1999, fire ants were observed in a vireo nest at 11:17:02 CST while the adult female was apparently sleeping and incubating her clutch of four eggs. The nest was 1.05 m high in a shin oak (*Quercus sinuata* var. *breviloba*). The female vireo started to peck at the ants 5.22 min after they arrived at the nest. Beginning 15.27 min after the arrival of the ants, the female perched on the rim of the nest and rapidly pecked to remove the ants. She actively removed ants for 2.05 min, after which she abandoned the nest and was not observed again.

An eastern woodrat approached and inves-

tigated the exposed clutch of eggs 0.83 min after the female abandoned the nest. While fire ants were present on the nest and eggs, the woodrat made physical contact with the eggs but did not depredate any of them. The woodrat remained at the nest for 0.37 min before leaving. Ants continued to swarm the nest both during and after the time that the woodrat was at the nest.

Shortly after sunrise (05:30:02) the next day, an adult male vireo arrived at the nest while fire ants continued to swarm the clutch. He immediately engaged in aerial defense of the nest. He continued this behavior for 24.97 min before attempting to incubate the clutch. The male switched between incubating and rapid pecking behaviors for another 24.03 min before abandoning the nest. At the time of abandonment, fire ants remained at and continued to swarm the nest. Despite the failed predation attempt by the woodrat and nest defense by the adult vireos, the ants remained at the nest for a total of 29.55 hr. The clutch failed to hatch. Careful examination of the eggs later revealed that one egg had a small hole in it. The egg was presumably nicked by the woodrat as fire ants are apparently unable to puncture intact egg shells, though they do forage on pipped or cracked eggs (Ridleyhuber 1982, Buhlmann and Coffman 2001; this study).

At another vireo nest containing three, 8-day-old nestlings, an adult female vireo was last seen at 19:36:59 on 16 June 2000. This nest was located 0.74 m high in a Texas oak (*Q. buckleyii*). Fire ants swarmed the nest at 01:03:38 on 17 June, while all three nestlings were apparently sleeping and no adult birds were present. Beginning 16.70 min after the ants were first observed at the nest, the nestlings began to squirm and move frantically from side to side and continued to do so for the next 3.55 hr. At 04:48:20, a rat snake arrived at the nest, which was still swarming with ants. The snake investigated the nest for 2.65 min before striking and consuming a vireo nestling at 04:50:59. The snake proceeded to depredate the other two nestlings at 04:57:57 and 05:03:00 (9.62 min and 14.67 min after arriving at the nest). The snake did not appear to be affected by the ants. The snake left the nest at 05:15:04, with ants continuing to swarm the now empty nest.

At 05:18:05, an adult female vireo returned to the empty nest, where ants were still swarming. She engaged in aerial defense for 15.58 min until an adult male vireo arrived at 05:33:40. At this time, both adults continued to defend the nest, alternating in aerial defense of the nest. Fire ants were last observed at the nest at 07:05:31 and both adults abandoned the nest at 07:06:43.

DISCUSSION

Fire ants caused nest failure during this study by swarming vireo nests (resulting in nest abandonment) and by direct predation of nestlings. Our two observations of behavioral interactions between predators suggest that fire ants may contribute both positively and negatively to the nesting success of vireos. In two predation attempts, fire ants apparently deterred a mammalian predator, but not a snake, from depredate a vireo nest.

Because fire ants also impact other species, including those that may depredate vireo nests, there are a number of possible indirect effects of fire ants on vireos. Fire ants may indirectly reduce rodent populations through competition for common food sources (Killion et al. 1995, Ferris et al. 1998). Fire ants are known to prey upon small mammals (Killion et al. 1995, Ferris et al. 1998), and they may alter small mammal habitat use (Pedersen et al. 2003) and foraging patterns (Holtcamp et al. 1997) in ways that deter rodents from depredate vireo nests. Fire ants depredate piped eggs and hatchlings of reptiles (Mount et al. 1981, Tuberville et al. 2000, Buhlmann and Coffman 2001, Parris et al. 2002), which could alter snake densities and, ultimately, rates of vireo predation.

Other indirect effects may result from the interaction between fire ants and vireos themselves. When fire ants swarm vireo nests, they induce alarm responses from adult and nestling vireos. Aerial defense by adults, and panic response by nestlings, may attract other predators, including snakes, to the nest. Although fire ants apparently are unable to breach intact eggs (Ridleyhuber 1982, Buhlmann and Coffman 2001, Stake and Cimprich 2003), they are able to depredate young vireo nestlings (Stake and Cimprich 2003).

Fire ants negatively affect nest success directly via depredate and abandonment; both

positive and negative indirect effects are also likely. Study of the potential indirect effects of fire ant depredate of vireos and co-occurring bird species should be a component of future studies of bird/fire ant interactions.

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PREDATION RISK ASSOCIATED WITH GROUP SINGING IN A NEOTROPICAL WOOD-QUAIL

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ABSTRACT.—Decades of fruitful research on the study of vocal communication in birds have provided surprisingly little evidence of a predation cost associated with singing. In this paper, I report the first observational evidence of a risk of predation associated with chorusing in a Neotropical wood-quail. Black-breasted Wood-Quail (*Odontophorus leucolaemus*) live in groups year-round and produce coordinated group choruses or duets. Three mammalian and two avian species of predators were attracted to playbacks of recorded wood-quail choruses that I used during population surveys and capture attempts from March to August, 2000–2002. The trade-off between signaling and predation risk may be an important force in the evolution of chorusing in New World quails. Received 12 February 2004, accepted 19 July 2004.

Long distance vocalizations are used for territory defense, mate attraction, and other functions in a variety of animals (Bradbury and Vehrencamp 1998, Todt and Naguib 2000). Whenever such signals are sent, however, there is a danger that they will be heard and taken advantage of by illegitimate receivers, such as competitors, parasites, or predators (McGregor 1993, Bradbury and Vehrencamp 1998, Haynes and Yeargan 1999). For example, the parasitoid tachinid fly, *Ormia ochracea*, is attracted to tape recordings of a host cricket, *Gryllus integer* (Cade 1975); the fringe-lipped bat (*Trachops cirrhosus*) uses acoustic cues to capture calling frogs (Tuttle and Ryan 1981); and several species of foliage-gleaning bats in Panama use the mate-attracting songs of male katydids to locate these prey (Belwood and Morris 1987). In birds, however, evaluation of predation costs associated with signaling has primarily been restricted to studies of plumage conspicuousness (Gotmark 1992, Promislow et al. 1992, Andersson 1994). Although most studies of costs associated with vocal communication in birds have focused on energetics (Eberhardt 1994, Oberweger and Goller 2001, Thomas 2002), eavesdropping by predators has been demonstrated experimentally in three species. The first experimental evidence comes from a study of Red-winged Blackbirds (*Agelaius phoeniceus*), in which nests accompanied by playback of female 'chit' calls were depredated at higher rates than nests without playback

(Yasukawa 1989). Two recent studies provide additional experimental support: Brown Skuas (*Stercorarius antarctica*) use the mate attraction calls of colonially nesting seabirds as a cue for prey location and selection (Mougeot and Bretagnolle 2000), and long-distance calling in Crested Tits (*Parus cristatus*) increases the risk of predation by Eurasian Sparrowhawks (*Accipiter nisus*; Krams 2001).

In this study, I report observational evidence that predators are attracted to group singing in Black-breasted Wood-Quail (*Odontophorus leucolaemus*), a social species restricted to the remaining highland forest of Costa Rica. Black-breasted Wood-Quail live in coveys year-round (2 to 15 individuals) in the dense understory of cool, wet forest between 900 and 1,600 m elevation. Nesting usually occurs around the onset of the rainy season in May and June (McDonald and Winnett-Murray 1989; AMH pers. obs.). Coveys defend group territories and produce coordinated group choruses or duets. Neighboring coveys are most often heard calling back and forth just after dawn. All members of the covey participate in the chorus, and individuals often hop up on perches (dead fallen trees) approximately 1 m off the ground while singing. Depending on the weather and terrain, the chorus is audible to humans from a distance of 200–500 m (AMH pers. obs.). Because choruses and duets by a single mated pair have the same basic structure in Black-breasted Wood-Quail, hereafter I will refer to both as choruses.

METHODS

The study area is located in Monteverde (10° 15' N, 84° 46' W), a 1,500-ha dairy farm-

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ing community at an elevation of 1,350–1,500 m on the Pacific slope of the Cordillera de Tilarán in Puntarenas Province, Costa Rica. This area is the site of long-term ecological studies and has been well described (Nadkarni and Wheelwright 2000). Monteverde is a fragmented landscape, composed of open pastures, some cultivated bananas and coffee, and considerable remnant pre-montane and lower montane moist/wet forest (Holdridge 1967). The community lies on a narrow plateau bounded on the north by human dwellings and agriculture, on the south and west by cliffs, and on the east by a large expanse of cloud forest—the 28,000-ha Monteverde Reserve Complex, Costa Rica's largest intact highland forest. Black-breasted Wood-Quail inhabit the large windbreaks and patches of remnant forest in the Monteverde community and the continuous forest of the Monteverde Reserve Complex. Although locally common in the Monteverde area, Black-breasted Wood-Quail are generally rare throughout Costa Rica (Stiles and Skutch 1989, Fogden 1993), and are classified as a species of conservation concern by the IUCN—World Conservation Union (Collar et al. 1994, Fuller et al. 2000). In Monteverde, average covey size is four adults with approximately 77% of surveyed coveys containing three or more adults ($n = 151$ coveys). Average density is one covey per 3.3 ha (AMH unpubl. data).

From March through August, 2000–2002, I conducted wood-quail surveys in the Monteverde area by using playbacks of choruses to simulate territorial intrusions. A single recording from the *Indicator Birds of the Costa Rican Cloud Forest* CD (Ross et al. 1997) was used in 2000 and 2001. This 58-sec recording consisted of three choruses from a bout of counter-singing between two coveys of unknown size. The recordings used in 2002 were obtained from songs provoked by the use of playback. Recordings were made from 64 bouts of singing by 45 coveys; I used a Sony Cassette Recorder TC-D5M and Audio-Technica unidirectional microphone (70–18,000 Hz). Digital sound files were created from the analogue recordings at 22.05 kHz with 16-bit accuracy using Syrinx Version 2.2b (2001). Sixteen experimental tapes, consisting of one chorus each from 16 coveys of known size (range 2–7 adults), were made to

determine whether wood-quail coveys adjusted their responses to playbacks based on the number of individuals in the “intruding” covey. These 16 choruses were chosen based on the clarity of the recording and the absence of other sounds, including singing by other species, wind, and rain. One of these tapes consisted of a 15-sec chorus that was looped to make a 30-sec recording, while each of the other tapes consisted of a single chorus lasting 26–31.5 sec.

To simulate territorial intrusions, I entered a group's territory and played a recording (30 sec from the cloud forest CD recording in 2000 and 2001, or one of the experimental tapes in 2002) using a Sony walkman, a 20-watt RMS power amplifier, and a 12.5-cm, 15-watt Speco loudspeaker (300–15,000 Hz) placed 0–2 m above the forest floor. If the group responded immediately, either by calling or approaching the loudspeaker, I did not continue with playback. If the group did not respond, I repeated the playback once every 3 min for a maximum of 15 min. Amplitude level of the playback was matched by ear to singing wood-quail and was held constant throughout the trials. In general, the playback was just loud enough so that the sound traveled approximately 200 m and was not distorted. Wood-quail coveys tended to respond immediately when a recording was played within their territories; they would sing and approach within a few cm of the loudspeaker. Solitary individuals also responded to playbacks by singing, but did not closely approach the sound source. I also used playbacks to lure wood-quail into mist nets or large traps for individual marking and genetic sampling. The number of times the recording was played during capture (from 1 to approximately 20 times per hr) depended upon the response of the focal group and the number of group members captured.

RESULTS AND DISCUSSION

Wood-quail choruses are rushing gabbles of notes patterned into two sets of paired syllables that are repeated over and over. Choruses last 10–60 sec and occur most often just after dawn (54% of spontaneous choruses occurred between 05:30 and 06:30 GMT-6, $n = 87$ choruses). The majority of choruses are answered by neighboring groups, and bouts of counter-

singing among neighbors last from about 1 min to over 1 hr (AMH unpubl. data). When two or more social groups come into contact near a territorial boundary, each group produces a well-coordinated chorus and the groups will either alternate or overlap their bouts of singing. Often, after a few bouts of counter-singing, one or more groups will retreat from the area. In other instances, the territorial encounters can last up to several hr. In addition to continued singing during territorial encounters, individuals produce several other vocalizations and participate in strutting displays, chases, and even physical fights with neighboring group members. Wood-quail coveys responded to simulated territorial intrusions with either choruses or approaches during 65% of surveys and 75% of capture attempts in 2000–2002 ($n = 467$ surveys and $n = 122$ capture attempts).

During surveys and capture attempts, I witnessed eight instances of predator response to playbacks of wood-quail choruses (three in 2000, four in 2001, and one in 2002). During 109 survey mornings (mean = 4.3 social groups surveyed per morning), the loudspeaker was approached by a single predator on four occasions: two gray foxes (*Urocyon cinereoargenteus*) and two Collared Forest-Falcons (*Micrastur semitorquatus*). These predators approached the loudspeaker after the recording had been played from one to three times. During 95 capture mornings, the loudspeaker was approached on three occasions by a single predator, one margay (*Leopardus wiedii*), one Barred Forest-Falcon (*Micrastur ruficollis*), and one Collared Forest-Falcon, and on one occasion by two domestic dogs (*Canis familiaris*; which have been observed to capture wood-quail in this area). While the forest-falcons approached the loudspeaker after the recording was played just three times during capture attempts, the margay and dogs responded after the recording had been played approximately 10 times. In each of these instances, the behavior of the predator suggested that it was responding to the vocalizations rather than something else in the environment. The two foxes walked directly to the loudspeaker before leaving the area upon seeing me; the margay broke through the mist nets and pounced on the loudspeaker; one Collared Forest-Falcon landed within a few m of the

approaching covey and pursued the quail on foot as they ran for cover; two Collared Forest-Falcons and the Barred Forest-Falcon perched on a branch located approximately 3 m above the loudspeaker and visually searched the immediate area; and the dogs ran directly at the loudspeaker before pausing and searching the surrounding area. Two of these predators are forest specialists (Collared Forest-Falcon, margay) and may be constrained to using vocal cues to locate prey. Unlike the other predators, the Barred Forest-Falcon is too small (165–200 g; Stiles and Skutch 1989) to capture adult wood-quail (mean = 295 g \pm 16 SD, $n = 103$ adults; AMH unpubl. data); however, because these playback trials occurred during the wood-quail breeding season, it may have been looking for chicks.

Although energetic costs associated with producing signals have received the most attention, there is increasing evidence that additional costs, such as increased exposure to predators, should also be considered in studies of the evolution of communication (reviewed in Gil and Gahr 2002). This may be particularly important in birds because the empirical evidence for a high energetic cost of singing in passerines is equivocal (Eberhardt 1996, Gaunt et al. 1996, Oberweger and Goller 2001, Thomas 2002, Ward et al. 2003), and studies of a nonpasserine, Red Junglefowl/domestic roosters (*Gallus gallus*), show that crowing is not energetically costly (Chappell et al. 1995, Horn et al. 1995). Similarly, chorusing in Black-breasted Wood-Quail seems unlikely to be energetically costly even though it is a year-long endeavor: on any given day, individuals sing for a short amount of time, perhaps giving only several bouts, each less than 1 min in length (AMH unpubl. data). This is in contrast to the high level of singing effort, in terms of both frequency and duration of songs, observed in many male passerines during the breeding season (Welty 1982, Catchpole and Slater 1995). This comparison suggests that a high metabolic cost and loss of time that could be spent foraging or resting are not likely for wood-quail, with the exception of chorusing associated with prolonged territorial encounters.

The observations presented here suggest that predators eavesdrop on choruses produced by wood-quail. In my study area, a

predator responded to recordings on 1.4% of the 589 surveys or capture attempts. This is likely to be a great underestimate of the risk of predation; it is reasonable to presume that I did not see all of the predators that were attracted to the playbacks, in part because they avoid humans. Moreover, the suite of detected predators included both those that are commonly seen (e.g., Barred Forest-Falcon, gray fox) and those that are observed only rarely in the Monteverde area (e.g., Collared Forest-Falcon, margay) (Fogden 1993, Nadkarni and Wheelwright 2000). Detection of these rare or uncommon predators provides further support that the potential suite of predators is large and that chorusing in Black-breasted Wood-Quail may have a non-trivial cost of predation. Additional anecdotal evidence suggests that the risk of predation associated with chorusing will be even greater during territorial encounters because of increased amounts of singing and impaired vigilance. In the few cases in which I was able to closely observe territorial encounters, I successfully approached the wood-quail to within a few m without being detected. Future playback studies should reduce variation in the amount of signal that is available to potential predators from one playback trial to the next, and incorporate a control (i.e., recordings of silence or other sounds) to account for the likelihood of detecting a predator by chance. These modifications would improve the estimate of the frequency of eavesdropping and confirm its relative importance in this system.

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RITUALIZED AGGRESSION AND UNSTABLE DOMINANCE IN BROODS OF CRESTED IBIS (*NIPPONIA NIPPON*)

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ABSTRACT.—In broods of Crested Ibis (*Nipponia nippon*), aggressive dominance was unstable over time, even within feeding sessions. All chicks took turns pecking aggressively while broodmates hung their heads submissively, although roles were contested at the start of feeding bouts when chicks were 11–17 days old. In all broods, at least half of all pecks were *false pecks*, which did not strike broodmates even when within reach. False pecks seem to be ritualized displays that function to solicit food from parents and possibly to threaten rivals. Received 9 July 2002, accepted 24 March 2004.

We describe an extraordinary form of agonistic interaction between broodmates of the Crested Ibis (*Nipponia nippon*), a critically endangered ciconiiform (Liu 1981). Aggression among altricial broodmates occurs in a variety of avian taxa, including some ibises, egrets, raptors, boobies, anhingas, guillemots, and kingfishers (reviews in Mock 1984, Mock and Parker 1997, Drummond 2002). Generally, broodmate hierarchies are formed through pecking and biting (review in Drummond 1999), and, in species where siblicide is facultative (Lack 1947, 1954; Ricklefs 1965), the intensity of aggression varies with the amount of food provided by parents (Drummond 2001a, 2001b; but see Mock et al. 1987, Forbes and Mock 1994). Threatening postures and calls are common (Drummond 2001b), but no species has been reported to show ritualized attacks that do not impact the victim.

The Crested Ibis feeds on loaches, eels, locusts, and freshwater invertebrates, including insects, and lays two to four eggs in a tree nest; eggs hatch at 1- to 2-day intervals (Zheng 1973, Li and Huang 1986). Both parents feed the chicks by regurgitation until the chicks become independent at about age 70

days, 4 weeks after departure from the nest. Because of food competition, broods of most ibis species are facultatively reduced to two fledglings (Matheu and del Hoyo 1992), but brood reduction is relatively uncommon in Crested Ibis: 78.3% of hatchlings fledge (Zhai et al. 2001), compared to 56% \pm 14.1 (SD) that fledge in 29 bird species with parental feeding and a modal clutch size greater than one (reviewed by Royle et al. 1999).

We recorded ibis behavior at hillside nests in Shaanxi Province (33° 18' N to 33° 24' N and 107° 23' E to 107° 28' E), China. Observers sat upslope of the colony at vantage points 15–50 m away from nests and watched broods through a telescope from 07:00–19:00 UTC + 08. Hatching order (a-chick, b-chick, and so on) was evident from marked differences in body size that persisted throughout the nestling period (as in the Bald Ibis, *Geronticus eremita*; Hirsch 1979). In 1999, we recorded behavior at nest 9918, where two broodmates, which hatched 2 days apart, were visible from a vantage point 30 m away. We observed behavior daily between hatching and fledging 41 days later, recording all feeding sessions on video. In addition, we observed seven broods of two, three, or four chicks ($n =$ one, five, one broods, respectively) on 16 days (2.7 days/brood) in 1997, 1998, and 2000, when broods were in Stage 3 (>18 days old).

We recorded the absolute frequencies of *feeds* and *pecks*. During each parent's period of nest attendance, it typically fed the brood in a single session of two to eight regurgitations. Each regurgitation elicited a bout of chick aggression and a single feed. A feed was recorded whenever a chick received food by

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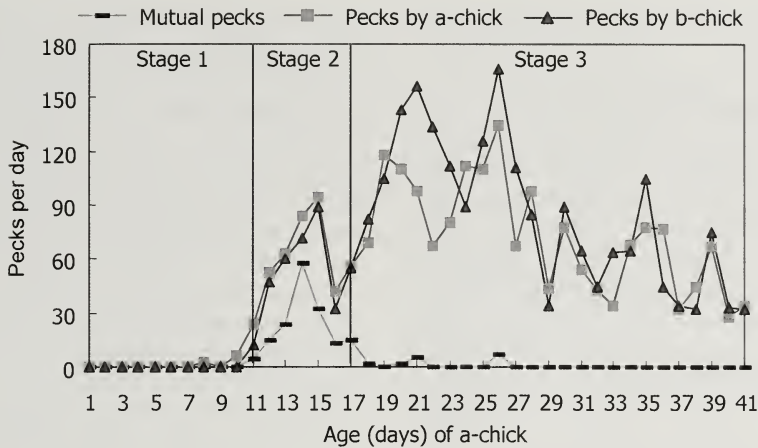


FIG. 1. Rate of pecking at a Crested Ibis (*Nipponia nippon*) nest, Shaanxi Province, China, 1999. The two chicks (brood 9918) pecked at similar rates, taking turns at aggressive pecking.

inserting its bill (usually its whole head) into the parent's bill. Pecks included any rapid downward thrust of the head, including *real pecks*, where open bill tips struck the broodmate (usually on the head or nape), and *false pecks*, where no target was struck and the downward thrust ended at the nest floor. The two categories of pecks were recorded simply as pecks because we often could not tell whether a peck was real or false. When the chicks at nest 9918 were aggressive during a bout (*mutual pecking*), they pecked at similar frequencies and it was difficult to count all pecks; thus, we counted only the mutual pecks of the more visible chick. Pecking frequencies of brood 9918 were recovered from video recordings, and those of the seven broods in Stage 3 were recorded using a hand counter. Video recordings were transferred from tape to Audio Video Interleave files using a VideoKing™ video compress card (Beijing Kefa Electronic Co. 1997), and those files were analyzed using Adobe Premiere 5.0 (Adobe Creative Team 1998).

Development of aggression and feeding.—In brood 9918, we categorized development of feeding and agonistic behavior into three stages, according to the age of the a-chick. During Stage 1 (0–10 days old), agonism was absent. During Stage 2 (11–17 days old), arrival of the parent at the nest was followed by a bout of begging and mutual pecking until one chick (a or b) submitted by hanging its head low, whereupon the other (aggressive)

chick pecked for several seconds and the parent offered food to it. Sometimes, while the chicks were exchanging mutual pecks, the parent offered its open bill to one of them, which then fed. After submission by one chick, the other chick seemed to diminish its attacks. In Stage 3 (18–41 days old), upon arrival of the parent, one chick (a or b) started pecking and the other usually responded by hanging its head submissively. The aggressive chick then begged and was fed one or more times, all the while continuing to peck its unfed nestmate until the latter started to peck the aggressive chick and beg for food. Then the fed chick promptly hung its head submissively, and the unfed chick received the next feeding.

Chicks of brood 9918 begged, without vocalizing, by raising their bills and repeatedly tapping the parent's bill. Pecks at the broodmate usually were accompanied by simultaneous chirping, which occurred in no other context and was interpreted as a threat call. Aggression by both chicks of brood 9918 increased more or less steadily throughout Stage 2 and during the first 10 days of Stage 3, before declining steadily over the last 15 days of Stage 3 (Fig. 1). Parents provided 5.3 ± 0.8 (SD) feeding sessions per day, with 4.1 ± 2.1 regurgitations per session. Adults did not obviously interfere in broodmate aggression and tended to feed whichever chick was begging. Over the 41-day nestling period, the a-

chick received 483 feeds and the b-chick received 451 feeds.

In the other broods, all of the chicks showed aggressive pecking on every day of observation. This followed the pattern of brood 9918 in Stage 3, with chicks taking turns pecking and begging while their broodmates hung their heads submissively; there was no clear consistency with respect to which fed first or more frequently. Whenever a chick pecked, it pecked at all of its broodmates. There was no significant difference in the daily feeding frequencies of a-chicks and b-chicks (13.7 ± 4.7 and 12.3 ± 3.6 feeds, respectively; Wilcoxon rank sum test, $Z = 0.93$, $P = 0.35$, two tailed, $n = 7$) or of a-chicks, b-chicks, and c-chicks (12.3 ± 1.2 , 12.1 ± 2.8 , and 11.4 ± 3.3 feeds, respectively; Kruskal-Wallis test, $\chi^2 = 1.31$, $P = 0.52$, $n = 6$).

Dominance.—Dominance occurred when one chick was aggressive and the other adopted a submissive posture. Although a chick often dominated its broodmate briefly, dominance between chicks was unstable over time, even within feeding sessions. In brood 9918, over the 41-day nestling period, the a-chick pecked its broodmate 53.6 ± 39.4 times a day, versus 59.5 ± 48.5 pecks by the b-chick (excluding mutual pecking). In Stage 2, neither chick tended to dominate first and get the first feeding. Sometimes when the b-chick was pecking aggressively and about to be fed, the a-chick rose up and, using its superior height, intercepted the feed. In Stage 3, chicks were only fed while temporarily dominant, and similar feeding rates of the a-chick and the b-chick (XL unpubl. data) reflect similar frequencies of temporary dominance by the two broodmates. In most feeding sessions a single chick maintained dominance throughout, but successive dominance was also common. Thus, in Stage 3, 68% of the a-chick's 152 feeds were obtained in sessions where the a-chick dominated throughout or initially, and 32% in sessions where the b-chick dominated initially; for the b-chick's 171 feeds, the b-chick's corresponding values were 64 and 36%, respectively.

Similar absence of stable dominance appeared to be the rule in all dyads of the seven broods observed in Stage 3. For each brood we calculated the mean number of times each

chick pecked its broodmates. The a-chicks and b-chicks (all broods) did not differ (86.8 ± 36.2 and 78.3 ± 31.4 pecks/day, respectively; Wilcoxon rank sum test, $Z = 0.886$, $P = 0.38$, two tailed $n = 7$). The a-chick, b-chick, and c-chick of each brood did not differ either (81.9 ± 25.0 , 72.6 ± 21.5 , and 73.1 ± 23.6 pecks/day, respectively; Kruskal-Wallis test, $\chi^2 = 2.02$, $P = 0.36$, $n = 6$).

False pecks.—False pecks included the threat call and frequently passed within centimeters of the broodmate, but they also occurred when the broodmate was out of range. Despite the victim being immediately in front, the aggressor directed pecks toward its own flanks, to one side and then the other, clearly avoiding the easy target (which might be standing with head lowered in submission) and striking nothing. False pecks occurred in all eight focal broods, and they appeared to represent roughly 60–70% of total pecks in brood 9918 and more than half of total pecks in each of the other seven broods. During mutual pecking, false pecks decreased to <10% of total pecks. False pecks occurred in Stages 2 and 3, usually after ordinary begging failed to elicit parental feeding. They could occur in the absence of genuine pecks at the broodmate, but they were almost invariably performed by the chick that currently dominated its broodmate. After fledglings departed the nest, real pecks were rare because victims promptly fled. False pecking continued during the next 4 weeks (when parental feeding was supplemented by attempts at self-feeding), even when the broodmate was out of sight. Like begging and real pecking, false pecking never occurred in the absence of a parent, and when false pecks occurred, parents offered food exclusively to the aggressor.

False pecking appears to be a ritualized form of real pecking, and both forms of pecking may elicit parental feeding. Originally, selection may have favored parents feeding aggressors, either because dominant chicks are more worthy of investment or because appeasing aggressors is a way of protecting their broodmates (when aggression is food dependent, Drummond 2001a). In either scenario, the door would be open for the evolution of signal function: parental feeding could be elicited initially by aggressive pecking and subsequently by false pecking. For the aggressor,

the advantage of using false pecks over real pecks may be that false pecks do less physical harm to the (long- and sensitive-billed) aggressor itself or to its sibling broodmate. Hence, false pecks could be more effective than ordinary begging for inducing regurgitation and ensuring feeding priority, and less costly than real pecks to the aggressor's individual and inclusive fitness.

Selection on parents to discriminate false pecks from real pecks would not necessarily result in parents declining to respond to false pecks. Discriminating parents could simply devalue the signal, responding to false pecks less than to real pecks (but more than to ordinary begging). Additionally, false pecking could be an especially potent signal if it also warns that violence will follow if food is not forthcoming or goes to the rival; it could deter rivals from begging, or blackmail parents into preferentially feeding the signaler. In brood 9918 at Stage 2, it seemed that whenever one chick begged during its broodmate's false pecking the broodmate responded by attacking more intensely, with real pecks.

False pecking may be associated with the Crested Ibis's unusual system of unstable broodmate dominance. Other aggressive brood reducers frequently attack even when food is not offered (Mock and Parker 1997), using real pecks to train broodmates into more permanent subordination (Drummond 2001b). For whatever reason, Crested Ibis chicks apparently attack only to secure immediate feeding priority, which may not require intense and extended violence.

Ultimately, false pecking may be related to the favorable ecological prospects of Crested Ibis broods, in which all young ordinarily fledge (Zhai et al. 2001). Because junior chicks do not usually face severe food shortage, they may pose only a negligible competitive threat to the survival of a-chicks, and as a consequence, a-chicks may be especially tolerant of them (Drummond et al. 2003). In Bald Ibis broods, however, frequent brood reduction signifies more severe food shortage (although chicks show successive dominance within feeding bouts, similar to the Crested Ibis); in this case, the order of dominance expression and access to food is dictated by a stable-dominance hierarchy and false pecking does not occur (Hirsch 1979, Oliver et al.

1979, Pegoraro and Thaler 1993, Tuckova 1999, Ros et al. 2001).

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Short Communications

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Incubation Period and Behavior at a Bar-tailed Godwit Nest

David J. T. Hussell^{1,2}

ABSTRACT.—Several standard references report the incubation period of the Bar-tailed Godwit (*Limosa lapponica*) as 20–21 days, but the source of those statements is unclear and may be based on speculation. Here, I report an incubation period at a nest in Alaska that was estimated to be between 21.7 and 23.8 days. This is consistent with incubation periods of three other species of godwit, which are reported to be 22–26 days. At the Alaskan nest, both sexes incubated and would not flush until approached within about 0.6 m. No special displays were observed when the male relieved the female at the nest. The chicks departed the nest when less than 1 day old. Received 28 October 2003, accepted 10 June 2004.

According to McCaffery and Gill (2001), the incubation period of the Bar-tailed Godwit (*Limosa lapponica*) is 20 to 21 days. Those authors cite Cramp and Simmons (1983) as their source. Cramp and Simmons (1983:479) state: "INCUBATION. 20–21 days. By both sexes but ♂ said to take major share (Witherby et al. 1940)." If their source for the incubation period was Witherby et al. (1940), then the 20–21 day period may be questioned. Witherby et al. (1940:157) give the incubation period as "about 3 weeks, but not definitely known."

Both sexes incubate, but there is conflicting information on which sex incubates most by day and night, and there is little information on changeover activities or on timing of departure of chicks from the nest (McCaffery and Gill 2001). Here, I report observations on the incubation period and behavior of Bar-tailed Godwits at a nest near Hooper Bay, Alaska.

In 1960, R. G. B. Brown, N. G. Blurton-Jones, and I spent approximately 3 months (early May to mid-August) in the vicinity of

Hooper Bay, Alaska (61° 35' N, 166° 05' W). We kept detailed records of all nests that we found and deposited them with the Alaska Nest Records Scheme at the University of Alaska Museum in Fairbanks.

Male and female Bar-tailed Godwits were easily distinguished when off the nest by the color of the underparts: mostly rufous-brown in the male and light gray-brown to white in the female. In the pair that we observed, the male was also noticeably smaller than the female.

Our first observation of a Bar-tailed Godwit occurred on 22 May at 18:00 AKST (subtract 2 hr 4 min to calculate Mean Solar Time), when we flushed a female off a nest containing three eggs. Although scattered pairs of Bar-tailed Godwits were seen throughout the area, we found no other nests. Our next visit to the nest was at 16:00 on 31 May, when we did not flush the incubating bird or determine its sex. On 1 June at 15:45, we flushed the male from the nest and found that it contained four eggs. On 13 June at 13:00, we noted that all four eggs were "just cracked." On 14 June at 15:00, the eggs were pipping "with one bill through" the shell of one of the eggs; at 22:00 that evening we found two newly hatched young and two eggs. On 15 June at 12:30, all four young were leaving the nest, with the female brooding them and the male standing guard nearby. Therefore, the fourth egg hatched between 22:00 on 14 June and 12:30 on 15 June. When the young departed the nest, the oldest and youngest chicks had been out of the egg for <22.5 and <14.5 hr, respectively.

We observed the male incubating on five occasions, at the following times: 15:45, 19:00, 19:00 (relieving the female, see below), 20:45, and 22:00 (with two newly hatched chicks and two eggs); mean = 19:18. The female was seen on the nest on seven occasions: 13:00, 14:00, 15:00, 17:00, 18:00 (with three eggs), 19:00 (relieved by male) and 19:30:

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mean = 16:30. Neither bird left the nest until we approached within about 0.6 m. Our observations were not randomly distributed throughout the day, so it is not possible to conclude that one or the other sex took the larger share of incubation during specific hours, but they do indicate that the male was often found on the nest in the evening and the female more frequently earlier in the day.

I watched the Bar-tailed Godwit nest from a blind for >2 hr during the afternoon of 11 June and recorded the incubating birds on 16 mm movie film. Initially, the female was incubating. She spent much of her time alert with her head partially or fully raised. At 20:00 the male relieved her. As he walked slowly toward the nest, the female called briefly and crouched low. He approached to within a few cm before she rose and flew directly from the nest. The male then settled on the eggs, facing in the opposite direction to the female's previous position. His subsequent behavior was similar to that of the female, alert with head raised.

The laying intervals of the Bar-tailed Godwit, the Marbled Godwit (*Limosa fedoa*), and the Hudsonian Godwit (*Limosa haemastica*) are unknown (Hagar 1966, Gratto-Trevor 2000, McCaffery and Gill 2001, Elphick and Klima 2002), but in the Black-tailed Godwit (*Limosa limosa*) the interval is 1–2 days (24–45 hr) with a clutch of four usually taking 5 days to complete (Cramp and Simmons 1983). Assuming that the laying interval in the Bar-tailed Godwit is approximately 1.5 days, the fourth egg in our nest was laid between 18:00 on 22 May and 06:00 on 24 May. These times indicate that the incubation period from laying to hatching for the fourth egg was between 21 days 16 hr and 23 days 18.5 hr. The mid-point of the range, 22 days 17.3 hr, is an estimate of the most probable length of the incubation period in this nest, given the preceding assumptions. If the laying interval was longer than 1.5 days and the female had laid her third egg shortly before we found the nest, the incubation period may have been shorter than 21 days 16 hr, but this seems unlikely.

My estimate of the minimum incubation period for this nest (21.7 days) is longer than the 20–21 days cited by Cramp and Simmons (1983) and McCaffery and Gill (2001). How-

ever, the latter period may be inaccurate if it is based on the speculative estimate of Witherby et al. (1940). My mean and maximum estimates (22.7 days and 23.8 days, respectively) are within the ranges reported for other godwit species: Black-tailed Godwit, 22–24 days (Cramp and Simmons 1983); Hudsonian Godwit, 23.5 days in one nest (Jehl and Husnell 1966); Marbled Godwit, little information but 23–24 days in one nest and “normally 24–26 d (M. Ryan unpubl. data)” (Gratto-Trevor 2000:13). It seems likely that the normal incubation period of the Bar-tailed Godwit is longer than 20–21 days and is probably usually within the 22–24 day range, as indicated for the nest reported here.

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Carnivorous Canada Geese

Joseph R. Jehl, Jr.¹

ABSTRACT.—Geese are normally herbivorous. I report an instance of Canada Geese (*Branta canadensis*) feeding on alkali flies (*Ephydra hians*) at hypersaline Mono Lake, California. The bout was brief and possibly represented exploratory behavior by inexperienced birds. Received 22 December 2003, accepted 25 May 2004.

Because geese are grazers and only rarely depart from their herbivorous diet, observations of their deliberate ingestion of animal matter are unusual. On 9 October 2003, at Mono Lake, California, I encountered seven Canada Geese (*Branta canadensis*) and three Greater White-fronted Geese (*Anser albifrons*) standing in a loose group on the upper beach, about 20 m from the water. Along the shore were a few Northern Shovelers (*Anas clypeata*) and Green-winged Teal (*A. crecca*). The geese were resting, but shortly four of the Canadas began slogging through knee-deep mud toward the shore, where adult alkali flies (*Ephydra hians*) had formed a thick mat. They then began to feed by orienting their bills parallel to the ground and scooping flies from the surface. The shovelers were doing the same at the water's edge, while the other Canada Geese and the White-fronted Geese showed no interest. As the day was cool, the flies were sluggish and could be captured easily. The geese fed leisurely for about 5 min, then returned to the upper beach and went to sleep. There was no doubt regarding their behavior; I could see flies being captured and ingested. Furthermore, the mudflats were devoid of vegetation; there was nothing else to consume.

Alkali flies are abundant on the shores of hypersaline lakes and constitute a major food for California Gulls (*Larus californicus*), Eared Grebes (*Podiceps nigricollis*), Wilson's Phalaropes (*Phalaropus tricolor*), Red-necked

Phalaropes (*P. lobatus*), and some ducks (Jehl 1988; JRJ pers. obs.), but they are ignored by geese. In more than 2 decades of observations at saline lakes, I have never seen any similar behavior. Indeed, reports of geese eating animal matter anywhere are exceptional, and the degree to which the few observations pertain to foods that might have been selected deliberately is open to question. Cottam et al. (1944:45) noted that animal food was occasionally found in the gizzards of Brant (*Branta bernicla*), but thought that it was probably "taken accidentally or incidentally." Subsequently, Bayer (1980) showed that Brant in Oregon took advantage of herring (*Clupea harengus*) spawns and fed deliberately on the eggs that were attached to vegetation, and Emperor Geese (*Chen canagica*) frequently feed on mollusks (Peterson et al. 1994). Canada Geese, however, are almost exclusively herbivorous (Owen 1980, Mowbray et al. 2002). Although other observers (e.g., Mickelson 1975:22; J. S. Seding pers. comm.) have reported goslings of Cackling Canada Geese (*B. c. minima*) feeding opportunistically on small flying insects, that behavior probably represents environmental sampling.

The observations on Brant differ from mine on Canada Geese in that Brant had learned to exploit a source of animal food (fish eggs) that was available only sporadically. Further, they fed heavily and in large groups (maximum 36 individuals), and relished eggs to the extent of pulling them from the bills of other species (Bayer 1980). Presumably the eggs provided the Brant, and mollusks provided the Emperor Geese, with significant nutrition. In contrast, both migrating and breeding Canada Geese at Mono Lake ignore alkali flies, even though they are predictable, available, and abundant through much of the year. Evidently, geese found the flies unpalatable because they fed on them briefly and without gusto, and the amount ingested could not have contributed much to their dietary requirements. At Great

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Salt Lake, Utah, alkali flies and waterfowl are far more abundant than at Mono Lake. Yet, I know of no reports of geese eating flies there or at any other saline lakes. I suspect that my observations were based on exploratory behavior by inexperienced juvenile geese.

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Intraspecific Predation among Northwestern Crows

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ABSTRACT.—Cannibalism is uncommon in birds, and instances of adults killing and eating other adults are especially rare. Cases of intraspecific predation among passerines constitute a very small percentage of published reports, and many of the cases are based on circumstantial evidence. In July 2001, I witnessed a group of Northwestern Crows (*Corvus caurinus*) kill and consume a conspecific adult in Olympic National Park, Washington. I am aware of no other published reports of adult-adult cannibalism for this species or the Corvidae family. Received 3 November 2003, accepted 27 April 2004.

Reports of cannibalism in which wild birds kill and consume conspecifics are uncommon; most instances have involved predation of eggs or young by adults (Stanback and Koenig 1992). Intraspecific predation among adult birds is especially rare and has been reported for only four species: Common Moorhen (*Gallinula chloropus*; Cawston 1983), Great Gray Owl (*Strix nebulosa*; Fisher 1975), Red-

tailed Hawk (*Buteo jamaicensis*; Clevenger and Roest 1974), and White Wagtail (*Motacilla alba*; Joslin 1964). Other than the White Wagtail report, I found no accounts of adult passerines killing and eating conspecific adults. Here, I describe my observation of a group of Northwestern Crows (*Corvus caurinus*) killing and consuming another adult.

The event described below occurred on 9 July 2001 near Tolbock Point in Olympic National Park, Washington. At 09:10 PST I heard a commotion in the forest approximately 30 m from the beach. A flock of about 15 Northwestern Crows were making loud and continual vocalizations similar to the mobbing call and dive-attack call described by Verbeek and Butler (1999).

Initially, I thought the flock was mobbing a predator, and I approached the group to investigate; at a distance of approximately 20 m, however, I saw that the flock was mobbing another Northwestern Crow perched on a branch about 3 m off the ground. I witnessed several crows swoop at the victim before one aggressor made hard physical contact and the two birds tumbled to the ground. From my position I watched as different members of the

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flock took turns swooping down to where the victim had fallen. Each aggressor stayed on the ground for only 2–3 sec before flying back to a perch and being replaced by another aggressor. Occasionally more than one aggressor was present on the ground at the same time, but for the most part, members of the flock took turns mobbing the victim.

My view of activities on the ground was obscured by the undergrowth, so after approximately 3 min of observing the mobbing, I approached the scene for a closer look. As I neared the victim, the aggressors retreated to adjacent perches, but continued their raucous calling. The victim was splayed on its back with wings spread and feet in the air. The crow was breathing heavily and following my movements with its eyes, but it made no attempt to flee as I approached. Other than lost feathers, the only visible injury was a large laceration on the right leg. The presence of a metallic gloss on the feathers of the head, throat, and breast indicated that the victim was not a juvenile, but either an immature or adult bird.

I returned to my original point of observation and the attacking group promptly resumed the mobbing. After 20 min, the activity began to decline substantially, and after another 10 min I approached the victim again. The crow was dead and the body cavity was empty. Because no tissue was found around

the carcass, it seemed evident that the attacking crows consumed the victim on the ground during the attack or carried parts of the victim away from the scene.

Intraspecific predation among adult birds has been well documented in captive birds, especially domestic hens, pheasants, and turkeys, and is thought to be correlated with the stressful conditions associated with captivity. Although rarely reported, the occurrence of adult-adult cannibalism in wild birds may not be unnatural, and could occur in response to stress, competition, or opportunity.

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White-winged Crossbills Obtain Forage from River Otter Feces

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ABSTRACT.—Instances of coprophagy by birds are rare in comparison to coprophagy by other animals such as mammals and insects. Here, I report on White-winged Crossbills (*Loxia leucoptera*) obtaining forage from river otter (*Lontra canadensis*) feces in Kouchibouguac National Park, New Brunswick, Canada. In sequence, two male White-winged Crossbills landed on a scat, pecked at it, and ingested small pieces before flying away. The birds may have been feeding on fish

bones or undigested fish present in the feces. *Received 28 October 2003, accepted 8 July 2004.*

White-winged Crossbills (*Loxia leucoptera*) mostly feed on seeds of spruce (*Picea* spp.), tamarack (*Larix laricina*), and sometimes fir (*Abies* spp.; Benkman 1987). When preferred seeds are scarce, they choose alternative foods, such as seeds from other conifers, deciduous trees, and grasses, as well as tree buds, insects, or spiders (Benkman 1992).

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Crossbills, predominantly the Red Crossbill (*Loxia curvirostra*), have been observed ingesting a great variety of rather odd items when supplementing their diet. Though data from captive Red Crossbills suggest that salt is not required in greater quantity than that found in their usual diet (Dawson et al. 1965), these birds regularly consume salt at various mineral sources in the environment. They have been observed obtaining salt by ingesting de-icing salt and sand spread on roads in winter (Lawrence 1982, Benkman 1992, Tozer 1994), mud in roadside pools (Tozer 1994), dog urine on snow (Manville 1941, Lawrence 1949), blocks of sulfurized salt kept for horses (Marshall 1940), and remains left from salt-pork barrels (Fisher 1888). They also have been readily attracted to saltlicks established by experimenters (Lawrence 1949, Bleitz 1958, Bennetts and Hutto 1985) and even by people harvesting them as a food source for subsistence (Fisher 1888). They can be approached easily when foraging for salt; Speirs (1985) observed them at his feet at a salt lick.

In addition to salt, crossbills are also attracted to sources of calcium. Observations of crossbills at calcium sources include calcium salts from cliff faces of andesite or pumice (Aldrich 1939), calcium chloride spread on a road (Meade 1942), fragments of calcium carbonate from a wall (Sainsbury 1978), putty from windows (Watson 1955), bleached deer bones (Baily 1953), and bone fragments from carnivore feces (Payne 1972). Crossbills also have been observed ingesting bits of charcoal (McMillan 1948), coal ashes (Lawrence 1949), and wood ashes (Tozer 1994). It is unclear whether the ash consumed in these instances is calcium-rich, as was the case for Ficken's (1989) observation of the same behavior exhibited by Boreal Chickadees (*Poecile hudsonica*). Lawrence's (1949) observations suggest that crossbills were probably attracted to coal ashes because salt had been thrown on them.

Crossbills are also known to ingest grit to help their digestion. They obtain it from various sources, such as the bases of uprooted trees (Benkman 1992), road cuts (Benkman 1992), mortar from stone chimneys and walls (Lawrence 1949, Bartlett 1976, Susic 1981, Tozer 1994), clay from the chinking in log houses (Nuttall 1903), or directly from the soil

(Nuttall 1903). Tozer (1994) interpreted that crossbills may also consume mortar for its calcium content. Another unusual observation is that of Red Crossbills being attracted to soapy dishwater (Lawrence 1949). Only Benkman's (1992) and Meade's (1942) observations (cited above) concern the White-winged Crossbill.

Coprophagy is not unusual among mammals (van der Wal and Loonen 1998, Hirakawa 2001) and insects (Hendrichs and Hendrichs 1990), but is rare in birds. Pale-faced Sheathbills (*Chionis alba*), for example, readily feed on pinniped feces (Favero 1996), and one Wilson's Storm-Petrel (*Oceanites oceanicus*) was observed feeding on feces of North Atlantic right whales (*Eubalaena glacialis*; Krauss and Stone 1995). The only two previous accounts of crossbill coprophagy include Red Crossbills ingesting bones from carnivore feces (Payne 1972) and a young Scottish Crossbill (*Loxia scotica*) feeding its sibling seeds obtained from feces (Nethersole-Thompson and Whitaker 1984). These observations are not examples of coprophagy in the strictest sense, however, since no actual digested fecal matter was ingested. Here, I report on two White-winged Crossbills obtaining forage from river otter (*Lontra canadensis*) feces. Observations were recorded in Kouchibouguac National Park in eastern New Brunswick, Canada (46° 47' N, 65° 01' W). The region is part of New Brunswick's lowlands, where the majority of forested areas are mixed, dominated by balsam fir (*Abies balsamea*) and birch (*Betula* spp.), or coniferous and dominated by black spruce (*Picea mariana*; Graillon et al. 2000).

On 7 March 2003 at 15:03 AST, while conducting shoreline transects for river otter, I observed two male White-winged Crossbills perched in a balsam fir near a river otter burrow. From a distance of 5 m, I watched one of the crossbills fly to an otter scat near the burrow and peck at the scat and ingest small pieces. After approximately 30 sec, the crossbill flew to a nearby tree; the second crossbill then landed on the same scat and pecked at and ate bits of the scat for <10 sec before flying away. My close proximity enabled confirmation of ingestion. Subsequent inspection of the scats confirmed that they were fresh,

unfrozen otter scats that contained several items of undigested fish flesh.

River otter defecation often results in large amounts of fecal matter concentrated in otter latrines (Testa et al. 1994, Bowyer et al. 1995, Swimley et al. 1998; DG pers. obs.). Because the visitation rate to latrines by river otters is high (Testa et al. 1994, Bowyer et al. 1995), and because scats thaw quite easily on sunny days (DG pers. obs.), feces could constitute an alternative food source for certain animals during winter.

It is possible that the two crossbills were trying to complement their diet by eating fish bones, which are numerous in otter scats, and would therefore constitute a ready source of calcium. Wild birds can be calcium deficient, which has been linked to adverse effects such as eggshell defects, clutch desertion, and empty nests (Graveland et al. 1994, Graveland and van der Wal 1996). Great Tits (*Parus major*), for example, do not obtain sufficient calcium from their usual diet of seeds and arthropods for adequate eggshell formation and skeletal growth (Graveland and van Gijzen 1994); they depend on snail shells as a complementary source of calcium (Graveland et al. 1994).

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Atypical Nest Site of a Semipalmated Plover

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ABSTRACT.—We report on an unusual nest site of a Semipalmated Plover (*Charadrius semipalmatus*) at La Pérouse Bay, Manitoba, Canada. The nest was located at the base of a 41-cm-high willow (*Salix* spp.) in a dense willow patch surrounded by coastal mudflats. Vegetation height and percent visual obstruction at the nest site were unusually high compared to height and cover previously described for Semipalmated Plovers. The nest was successful (≥ 2 eggs hatched). The discovery of this unusual nest site in dense vegetation suggests that some Semipalmated Plover nests may be overlooked, emphasizing the need to conduct thorough searches even in non-traditional habitats among shorebird species that typically nest in open habitats. *Received 9 October 2003, accepted 1 June 2004.*

Charadriidae shorebirds nest in unlined to thinly lined, shallow depressions in hardened clay or silt, or in loose stones, pebbles, or sand

in flat areas with sparse vegetation (Cooper and Miller 1997, Nol and Blanken 1999, Nguyen et al. 2003, Amat and Masero 2004). The disruptive effects of a plover's cryptic plumage and egg coloration against these substrates may enhance concealment from predators (Solís and de Lope 1995, Lloyd et al. 2000). Some plovers place their nests near objects or clumps of vegetation, which could provide microclimates that reduce thermoregulatory costs (Wolf and Walsberg 1996, Amat and Masero 2004). Cover, however, reduces visibility around a nest, which may result in a higher risk of predation compared to that of an exposed site (Koivula and Rönkä 1998, Amat and Masero 2004). Nest-site selection among shorebirds, therefore, may be a trade-off between needing security from predators, minimizing thermoregulatory costs, and having a view of the surrounding area (Wolf and Walsberg 1996, Koivula and Rönkä 1998, Amat and Masero 2004). Here, we report an unusual instance of a Semipalmated Plover (*Charadrius semipalmatus*) nesting in dense vegetation.

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On 17 July 2003, LPN and DL found the unusual Semipalmated Plover nest site at La Pérouse Bay, Wapusk National Park, Manitoba, Canada (58° 45' N, 93° 30' W). Several times we observed a plover entering a large patch (6.8 m long × 5.1 m wide) of willow (*Salix* spp.) surrounded by coastal mudflats. We found the nest, which contained four eggs, at the base of a willow. The nest was approximately 1.7 m from the outer edge of the willow patch and 10.2 m from the nearest water. RFR observed eggs and adults at the nest on 21 July; 2 days later, the nest contained two chicks and two eggs. On 25 July, neither adults nor young were observed in the immediate area.

We used a tape measure at each corner of a 1-m² quadrat frame to calculate mean height (41 cm) of vegetation within 1 m of the nest site. We used a transparent, 20 × 20 cm density board (100, 2 × 2 cm cells) placed vertically on the ground at the nest site to calculate mean percent visual obstruction by vertical cover (97%) between the nest and the four quadrat corners (Nguyen et al. 2003).

Previous descriptions of nest sites used by Semipalmated Plovers (Cooper and Miller 1997, Robinson 1998, Nguyen et al. 2003, Smith 2003) have not mentioned sites in densely vegetated habitat. Vegetation height and percent visual obstruction by vertical cover at the unusual nest site described herein were much greater than those at other Semipalmated Plover nest sites: Akimiski Island, Nunavut (5.8 cm and 21%, respectively, $n = 42$; Nguyen et al. 2003); La Pérouse Bay, Manitoba (0 cm and 38%, respectively, $n = 10$; RFR unpubl. data); and East Bay, Nunavut (12 cm and 6%, respectively, $n = 24$; Smith 2003). Although Cooper and Miller (1997) did not report vegetation height and percent visual obstruction by vertical cover at plover nests in the Queen Charlotte Islands, British Columbia ($n = 71$), they described nest sites on open sand, under elevated ends of logs or planks, and on gravel patches, all different from the nest site that we observed. Similarly, Robinson (1998) did not report specific nest-site characteristics at plover nests in Churchill, Manitoba ($n = 32$), but his descriptions indicated that nests were found primarily on gravel and stone, or lichen and moss, suggesting that vegetation height and percent visual ob-

struction by vertical cover were different from those at the nest site we observed.

Semipalmated Plovers that nest in open sites with little or no concealment from vegetation may benefit from good visibility and early detection of predators. If true, one would expect a low rate of success among nests in dense vegetation. However, previous studies have shown that nest cover—an indicator of visibility—does not affect shorebird nest success at typical nest sites (Koivula and Rönkä 1998, Nguyen et al. 2003, Amat and Masero 2004). Additionally, nest sites used for re-nesting by Kentish Plovers (*C. alexandrinus*) had greater nest cover than those sites where the initial nest was depredated (Amat et al. 1999). We are not certain whether the Semipalmated Plover nest we found was the result of a late-nesting or re-nesting attempt. The discovery of a nest in dense vegetation, however, indicates that some Semipalmated Plover nests may be overlooked during monitoring or nest searching. We recommend that search efforts be increased in habitats of dense vegetation to assess the frequency of nesting in those types by shorebird species that typically nest in open habitats.

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Song in Female *Hylorchilus* Wrens

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ABSTRACT.—We report on the discovery of a distinct female song in Nava's Wren (*Hylorchilus navai*), similar to that recently discovered in Sumichrast's Wren (*Hylorchilus sumichrasti*). In both species, females sometimes countersing with males but do not combine their songs into a synchronized duet as in many other tropical wrens. We provide observations that suggest territorial defense, intra-pair contact, and perhaps mate-guarding as possible functions of female song in *Hylorchilus*, a little-known genus endemic to Mexico. Received 12 December 2003, accepted 28 June 2004.

In the largely Neotropical family, Troglodytidae, females show a diversity of singing behaviors (Farabaugh 1982, Barker 2003). In some species, females do not sing regularly,

but in others female songs may be simple rattles (rapid repetitions of a single, low-pitched syllable), usually complementing their mates' more complex whistles. Female songs also may be sung in highly coordinated, whistled duets with their mates (Farabaugh 1982). Female rattles have been reported in Mérida Wren (*Cistothorus meridae*; Kroodsma et al. 2001), Carolina Wren (*Thryothorus ludovicianus*; Shuler 1965, Farabaugh 1982), House Wren [*Troglodytes aedon* (*musculus* group); cf. Skutch 1953, Farabaugh 1982, Sick 1993], Socorro Wren (*Thryomanes sissonii*; Howell and Webb 1995), and Sumichrast's Wren (*Hylorchilus sumichrasti*; Pérez-Villafaña et al. 1999). Here, we report on the discovery of female song in Nava's Wren (*Hylorchilus navai*) and provide observations on the context and possible function of female rattles in *Hylorchilus*, a little-known genus endemic to Mexico.

On 26 March 2002, while observing a singing male Nava's Wren at the type locality for this species northwest of Tuxtla Gutiérrez, Chiapas, Mexico (16° 56' N, 93° 27' W), HGdS and CAM heard and tape recorded a

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series of rapid whistles that they could not identify. Playback of this vocalization immediately provoked close approach by the male and the appearance of a second individual, a female, recognizable in the field based on her slightly shorter bill (cf. Crossin and Ely 1973) and the general resemblance of its song to that of female Sumichrast's Wren (see below). Soon, both birds began countersinging, and they continued to do so for several minutes. Countersinging is known to occur in Sumichrast's Wren (Pérez-Villafañá et al. 1999). Conceptually, it is sometimes difficult to distinguish bird songs from calls, but songs are usually given in the context of either territoriality or pairing behavior, whereas calls usually are not (Spector 1994, Langmore 1998).

Countersinging in response to tape playback suggests that female song in Nava's Wren is used in territorial defense for intra-pair communication during an agonistic event. As in the Sumichrast's Wren (Pérez-Villafañá et al. 2003), the posture adopted by the female Nava's Wren while singing was similar to that used by the male, with the body held upright and the bill raised. This posture, the loud nature of the song, and the fact that it was given by birds perched atop limestone boulders, suggest that the song may be used as a long-distance signal.

The song of the female Nava's Wren is an introductory note followed by a rapid series of eight or more loud, shrill whistles; the song rises slightly, remains relatively steady, and ends abruptly: "wup wick-wick-wick-wick-wick . . ." (Fig. 1A). Seventeen songs from a single bout of countersinging averaged 2.6 ± 0.6 sec (SD) in length and contained 14.9 ± 3.7 notes. Singing behavior appears to be similar in both species of *Hylorchilus*. As in countersinging pairs of Sumichrast's Wren (HGdS and MPV pers. obs.), the rate of song delivery in female Nava's Wren (5.4 songs/min) is somewhat slower than in the male (8.5 songs/min) and the individual songs are significantly longer in duration (female: 2.6 ± 0.6 sec, $n = 17$; male: 1.8 ± 0.1 sec, $n = 31$; t -test, $P < 0.001$). The song given by female Sumichrast's Wren is also a relatively steady series of notes, but notes are delivered at only about half the rate (Fig. 1B). Moreover, in female Nava's Wren the maximum fundamental frequency is higher (2.42 ± 0.08 kHz) than it

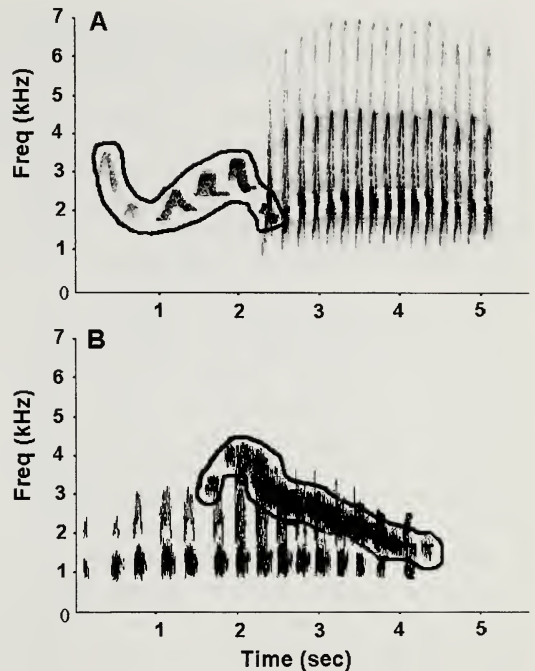


FIG. 1. Spectrograms of countersinging male and female *Hylorchilus* wrens. Contributions of males are encircled by solid lines. (A) Portion of a countersinging bout of Nava's Wren (*Hylorchilus navaei*) featuring slightly overlapping male and female songs. Recorded by CAM at the type locality of Nava's Wren in Chiapas, Mexico (see text), on 26 March 2002, using a Nagra 4.2 and a Sennheiser MKH-20 microphone mounted inside a Telinga Pro parabola (CAM field #2000-07-04 deposited at the Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, New York). The spectrogram was made using Syrinx, version 2.2K (www.syrinxpc.com). (B) Portion of a duet of Sumichrast's Wren (*Hylorchilus sumichrasti*) showing complete overlap between male and female song. Recorded by S. N. G. Howell 1.5 km south of Amatlán, Veracruz ($18^{\circ} 50' N$, $96^{\circ} 55' W$), on 21 September 1995 with a Sony TCS 430/450 and a Sennheiser ME66 microphone. The spectrogram was made using a Kay Elemetrics DSP Sonograph, Model 5500, in the sound analysis laboratory of L. E. Baptista, California Academy of Sciences, San Francisco.

is in the hoarse song of female Sumichrast's Wren (2–2.2 kHz). Unlike duets in many other wrens, the contributions of males and females in *Hylorchilus* are not highly coordinated or in synchrony. Instead, many male and female songs partly overlap. Successive female songs may begin near the beginning, middle, or end of the male's songs, with no apparent pattern. Indeed, some male songs in a duet do not

overlap female song. It may be that all female songs in a duet are overlapped by male song, but our sample is small; overlap would suggest mate-guarding as one function of male song. Song by female Sumichrast's Wren has been heard throughout the year (Pérez-Villafaña et al. 2003) and in a paired female without offspring (Pérez-Villafaña 1997), indicating that it is not related to coordination of biparental care (e.g., Langmore 1998).

Males of both *Hylorchilus* wrens frequently sing alone, and solo song by females has been recorded in the better-known Sumichrast's Wren. For example, Pérez-Villafaña et al. (2003) documented solo song by a paired female that was foraging and transporting nesting material. Females sing much less frequently than males (Pérez-Villafaña et al. 1999). Taken together with how little is known about *Hylorchilus* wrens, this may explain why it took so long to document female song in these species. Whereas the songs of male Sumichrast's and Nava's wrens were first described in 1987 and 1993, respectively (Hardy and Delaney 1987, Atkinson et al. 1993), female song was not described in Sumichrast's Wren until 1997 (Pérez-Villafaña 1997, Pérez-Villafaña et al. 1999), and until now, countersinging and female song had remained undescribed in Nava's Wren.

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We are grateful to S. N. G. Howell for allowing us to use his spectrogram of countersinging Sumichrast's Wrens, and the late L. F. Baptista for use of sonograph equipment. B. E. Daniels, J. L. Dunn, P. Ginsburg, G. McCaskie, and M. San Miguel provided companionship in the field when recording Nava's Wren. We thank A. Ríos Chelén and C. Macías for their help in measuring maximum fundamental frequency in Sumichrast's Wren songs, and D. E. Kroodsma and three anonymous reviewers for providing valuable comments on the manuscript.

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Ornithological Literature

Edited by Mary Gustafson

RELATIONSHIPS AMONG BODY MASS, FAT, WING LENGTH, AGE, AND SEX FOR 170 SPECIES OF BIRDS BANDED AT POWDERMILL NATURE RESERVE. By Robert S. Mulvihill, Robert C. Leberman, and Adrienne J. Leppold. Eastern Bird Banding Association (EBBA) Monograph No. 1. 2004: 184 pp.; 153 pp. of tables. \$15.00 (paper). Ordering information on EBBA Web site (<http://www.pronetisp.net/~bpbird/eb00009.htm>).— Considering the vast quantity of measurement data collected from birds during banding operations, it is quite surprising that so few summaries have been published. This monograph helps fill the gap, with analysis of 276,570 banding records for birds captured at Powdermill Nature Reserve (Rector, PA).

A short introduction describes data-collection methods and analyses. It provides a fairly complete and understandable description of data-collection methods and analyses, with a few exceptions. Notably, nothing is said about the methods used to determine age (skulling versus plumage or other characters). The explanation of how the tails of the wing-length frequency diagrams were adjusted is very unclear. However, the introduction is very good at pointing out caveats of which the user should be aware. For example, wing length was used to sex some individuals of some species, which affects the analyses of sex effects on wing length, and, appropriately, this is noted again in the summaries for the species so affected. Data were edited prior to analysis using various criteria for excluding outliers, which affects results by eliminating some valid data points, but the authors are clear on the methods used and warn users of the potential consequences.

The bulk of the document consists of tabular summaries of data. For all species with fewer than 10 records, the authors give complete data for each individual (age, sex, wing length, mass, and fat score). More abundant species have summaries of wing length and mass (sample size, mean and SD, minimum, and maximum), with the mass data subdivided

by fat score (using a fat scale of 0–3). These samples are further subdivided into age or sex categories for which there are five or more cases.

A particularly useful feature of the authors' analyses is that they did not define age groups using banders' designations of Hatch Year versus After Hatch Year. Rather, for body mass analyses, 'immatures' were defined as birds in their first 12 months of life (assuming a June hatch date), and, for wing-length analyses, 'immatures' were defined as birds having juvenal remiges (with a few well-explained exceptions). One of the interesting results from the book is that a high proportion of passerines have shorter wing lengths as immatures.

For the 100 species with sample sizes over 100, additional analyses were conducted. ANOVA was used to determine whether age or sex affected wing length or body mass (the latter analysis including fat class as a covariate). Regression of body mass on fat score provided estimates of lean mass and of the average fat mass for birds with a fat score of 3. Results were used to predict lean mass for each individual, which was regressed on wing length to describe the relationship between body mass and structural size (insofar as the latter is reflected by wing length). Graphics for each species summarize the proportion of birds in each fat class, and there are frequency diagrams of wing lengths for birds of known sex and for the total sample.

As is inevitable in a summary of this sort, there are limitations to what could be presented, and users must interpret results with appropriate caution. Data are not subdivided by time of year, and most summaries include data for birds from several seasons, mixing migrants and residents (proportion of the sample from each season is shown in an appendix.) Effects of age and sex on mass (with a fat score covariate) and wing length were analyzed separately in one-way ANOVAs; thus, interactions could not be detected. A useful addition would have been to include age, sex,

and season (if not month) as covariates in analyses, to show whether there are age-sex interactions and seasonal variation. Separate pie charts of fat score for each season would have proved interesting.

Because the regressions of body mass on fat score did not include age or sex as covariates, the resulting predictions of lean mass for each individual will be slightly off for species with age or sexual size dimorphism. In turn, this will have affected the predicted relationship of lean mass to wing length, which was calculated separately for each sex even though lean mass was calculated without respect to sex. The one-way ANOVA analyses showed significant age and sex effects on mass and wing length for most species, so there is likely to be more explainable variation in mass-body size relationships than has yet been teased out of the data.

The wing-length frequency diagrams will be of interest to many banders, although these, especially, require caution in interpretation. Wing length of known-sex birds was used to determine cut-offs useful for sexing (summarized in an appendix), but this will be appropriate only if the unknown-sex birds of each wing length have the same sex ratio as the individuals for which sex could be determined. The one-way ANOVAs also analyzed sex effects on wing length for only those individuals of known sex; thus, the magnitude and statistical significance of the effects may have been affected by sex bias in the sample of unknowns. Species varied dramatically in the proportion of unknown-sex individuals, but the frequency graphs often show data for known-sex and unknown-sex individuals plotted on very different scales, which obscures the true proportion of unknowns.

Despite the inevitable limitations, this volume is a fine source of basic data that are very difficult to find elsewhere, and which have a wide variety of applications in ecological studies. This monograph likely will inspire other banders to analyze their own data in a similar manner, or, perhaps, to concentrate on some of the questions left unaddressed by this volume. The authors indicate that their data are freely available to others for additional or comparative analysis, and this should facilitate direct comparison to demonstrate geographic variation.—ERICA H. DUNN, Cana-

dian Wildlife Service, Ottawa, Ontario, Canada; e-mail: erica.dunn@ec.gc.ca

EIGHTEENTH-CENTURY NATURALISTS OF HUDSON BAY. By Stuart Houston, Tim Ball, and Mary Houston. McGill-Queen's University Press, Montreal, Quebec, Canada. 2003: 333 pp., 49 maps and black-and-white photographs, 8 color plates, 7 tables, and 7 appendices. ISBN: 0773522859. \$49.95 (cloth).—This scholarly treatise highlights the accomplishments of a small group of men who worked for the Hudson's Bay Company (HBC) at trading posts during the 1700s, in an area that covered about half of modern Canada and, in places, dipped into what is now the United States. These men recorded weather observations and made natural history observations and collections that included birds. The collections were sent to Europe, where they were used by Linnaeus and others; thus, the efforts of the HBC group had a lasting impact on the history of ornithology. In 1974, the archives of the HBC were moved from England to Winnipeg, Manitoba, and were the main source of information for this book. Birds played a prominent role in the natural history records and collections and thus represent an important dimension in this book.

The book is divided into an introduction and 12 chapters that occupy the first 140 pages, followed by 7 appendices, extensive endnotes, references, and a comprehensive index. Seven associated documents that would have been too expensive to include in this volume are available online at the McGill-Queen's University Web site <http://www.mqup.mcgill.ca/books/houston/eighteenth-century>. The introduction provides background on the HBC, and Chapter 1 deals with the European natural history connection. This includes biographical materials on Sir Hans Sloane, George Edwards, Carolus von Linnaeus, Johann Reinhold Forster, Thomas Pennant, and John Latham, all of whom made use of bird collections and notes sent to Europe by HBC collectors. Chapters 2–9 present biographies of eight HBC men who made important contributions to the natural history of the substantial area controlled by the HBC. All played some

role in the history of ornithology. For example, Alexander Light brought back specimens to George Edwards, who portrayed them in his four-volume *A Natural History of Birds* (1743–1751), and Linnaeus described several as new species, including the Spruce Grouse (*Canachites canadensis*). James Isham also sent birds to Edwards, and Edwards' paintings became the type specimens for a dozen new North American species, including the Great Blue Heron (*Ardea herodias*). Humphrey Martin sent back specimens of a dozen species in 1771, including Eskimo Curlew (*Numenius borealis*), named by Johann Reinhold Forster the following year. He also was the first to put up nest boxes in Canada. In 1771, Alexander Graham sent back skins of 39 bird species, including the type specimens of Great Gray Owl (*Strix nebulosa*) and Blackpoll Warbler (*Dendroica striata*). Thomas Hutchins was a physician with broad interests in meteorology, physics, and natural history. His 1770s writings indicate that he was fully aware of the phenomenon of migration, and reported observations of food caching by jays. He was the only member of the HBC naturalists to have a bird named after him—Hutchin's Goose (*Branta canadensis hutchinsii*). Samuel Hearne was an observer rather than collector and made contributions to Thomas Pennant's *Arctic Zoology*, (1785). Peter Fidler was most interested in meteorology and cartography, but did make contributions to the understanding of long-term population cycles of arctic animals, including birds.

Chapter 10 provides discussion on various aspects of natural history involving members of the HBC, including sections on collectors, a chronology of 1770s collections, and a lengthy table that lists the birds of Hudson Bay and where they were mentioned in 18th century literature. It also has sections on the difficulties in preserving bird and mammal skins, the advent of Linnaeus' classification system, and the motivations of the HBC collectors.

The last chapter compares the Hudson Bay region with the Charleston, South Carolina area in colonial times; only the Charleston area surpassed the Hudson Bay region in terms of the number of North American natural history specimens collected. It includes a

discussion about Mark Catesby and a table listing new bird species that he described.

Seven appendices occupy 109 pages, four of which contain more than occasional references to birds. Appendix C is perhaps the most interesting. It concerns 10 manuscripts from the HBC archives that are attributed variously to Andrew Graham and Thomas Hutchins. The question of who wrote what, and what was copied from whom, has been bantered about for the better part of two centuries. Stuart and Mary Houston conducted some ornithological sleuthing to reveal the actual events, and the story of their adventure is presented in this appendix. The upshot is that, as a surgeon, Hutchins had better training than Graham, and his writing was more technical; hence, authorship of the manuscripts can be assigned on this basis, and it turns out that much of the work was collaborative. Appendix E deals with the 19th century trade in swan skins and quills that reached prodigious proportions in 1834, when nearly 8,000 reached European markets and likely contributed significantly to the demise of the Trumpeter Swan (*Cygnus buccinator*). Appendix F is a brief commentary on how the Canada Goose got its name before there was a Canada, and Appendix G—of which 25 pages deal with birds—is a long catalog of Cree Indian names for animals and plants in the 18th century.

This is a scholarly book (the endnotes alone occupy 61 pages) with much of interest for the historically inclined ornithologist. The nearly 500 references are indispensable to anyone interested in the history of North American ornithology and natural history. The book is well written and is interesting reading about a bygone era. Every academic library should have a copy of this book, as should anyone interested in the history of ornithology.—WILLIAM E. DAVIS, JR., Boston University, Boston, Massachusetts; e-mail: wedavis@bu.edu

BIRDS, SCYTHES AND COMBINES: A HISTORY OF BIRDS AND AGRICULTURAL CHANGE. By Michael Shrubbs. Cambridge University Press, Cambridge, United Kingdom, 2003: 382 pp., 36 line diagrams, 28 half-tones, 34 tables, 37 maps. ISBN:

0521814634. \$50.00 (cloth).—Michael Shrubbs is a retired farmer, historian, author, editor, and ornithologist. He began observing the interactions between farming and birds—and the effect of the one on the other—on his 234-ha family farm in West Sussex, where horses were used until 1952. Shrubbs has carefully researched the extensive history of British agriculture and farming methods, as well as all the 19th-century county and regional avifauna records for Scotland, Wales, and England. His exemplary, detailed research has produced a fact-filled book containing 34 informative tables and 37 excellent maps.

Harmful and destructive practices were common in the 19th century. There was a commercial trade in eggs of the Lapwing (*Vanellus vanellus*), Avocet (*Recurvirostra avocetta*), Oystercatcher (*Haematopus ostralegus*), Stone Curlew (*Burhinus oedicephalus*), and Black-headed Gull (*Larus ridibundus*). Trapping of Wheatears (*Oenanthe oenanthe*), netting of Skylarks (*Alauda arvensis*), and shooting of waders and waterfowl were widespread. Local populations of the Ruff (*Philomachus pugnax*) and Black-tailed Godwit (*Limosa limosa*) were exterminated early in the century. Goldfinches (*Carduelis carduelis*) were sold as cage birds.

Shrubbs describes the close and vital connections between agricultural practices and bird populations. Notable bird declines before the mid-19th century had varying explanations. As large tracts of sheep pasture fell to the plough, the Great Bustard (*Otis tarda*) disappeared by 1830, and the Stone Curlew lost nearly half of its range by 1900. With enclosure by hedges, healthier sheep and fewer sheep carcasses led to sharp declines in Red Kites (*Milvus milvus*), Common Buzzards (*Buteo buteo*), and Ravens (*Corvus corax*). With the advent of steam power to drain wetlands, Quail (*Coturnix coturnix*) numbers declined sharply and Bittern (*Botaurus stellaris*), Spotted Crane (*Porzana porzana*), Snipe (*Gallinago gallinago*), Ruff, Black-tailed Godwit, Avocet, Bearded Tit (*Panurus biarmicus*), and Savi's Warbler (*Locustella luscinioides*) suffered; somewhat paradoxically, the decline in Redshank (*Tringa totanus*) numbers began to reverse after 1870. Montagu's Harrier (*Circus pygargus*), Black Grouse (*Tetrao tetrix*), and Stonechat (*Saxicola tor-*

quata) failed to adapt to enclosure and cultivation. The Corncrake (*Crex crex*) and Whinchat (*Saxicola rubetra*) adapted poorly to the mechanization of haying. Control of weeds, especially thistle, led to declines in the Linnet (*Carduelis cannabina*) and Goldfinch, but expansion of orchards led to an increase in tits, Greenfinches (*Carduelis chloris*), and Bullfinches (*Pyrrhula pyrrhula*). Many of the species not mentioned above remained in more or less constant numbers until the Second World War.

Since then, widespread economic subsidies to farmers have affected the speed and scale of change. Together, the increasing size of farms, changes in grassland management, use of larger machinery, timing of cultivation, virtual disappearance of old-style crop rotations, and the use of pesticides to suppress weeds, have undermined the capacity of many species to adapt to farmland as breeding habitat. Lower survival of Gray Partridge (*Perdix perdix*) chicks, Yellowhammers (*Emberiza citrinella*), and Cirl Buntings (*Emberiza cirlus*) has been linked to declines in arthropods.

Rarely is it possible to attribute a change in populations or range to a single cause, but removal of 250,000 km of hedges may have been a factor in the decline of the Red-backed Shrike (*Lanius collurio*). Corvids and foxes have increased since about 1960, resulting in greater predation of ground-nesting birds. Increasing use of combine-harvesters since 1960 has decreased the amount of waste grain remaining, especially for wintering birds. Lapwings declined in the 1970s and 1980s when autumn-sown crops largely replaced spring-planted cereals.

Readers will find many helpful and thought-provoking parallels with North America, and will gain many insights about farm ecosystems and the way in which recent changes in agricultural practices, and even changes in farm buildings, have affected bird populations. My single criticism is that North Americans will have some difficulty with the agricultural terms well known to residents of Great Britain, especially farmers. For example, a sheepwalk is a sheep pasture; couch is couch grass; a wether is a male sheep. A glossary would have been a great help for such terms, as well as for ley, blanket mires, caddy

roof, chalking, marling, claying, ensiled, and mole draining.

Someone in North America might be tempted to emulate this book, even though England's rich collection of 19th-century avifaunas could not be matched here—nor are we yet able to compile bird population numbers as accurately as the annual Common Birds Census (CBC!) allows in Great Britain. This superb book demonstrates, perhaps better than any other, the value of historical studies in ornithology.—C. STUART HOUSTON, University of Saskatchewan, Saskatoon, Canada; e-mail: houstons@duke.usask.ca

VOICES OF NEW WORLD PARROTS. By Bret M. Whitney, Theodore A. Parker, III, Gregory F. Budney, Charles A. Munn, and Jack W. Bradbury. Macauley Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, New York. 3 CD set, 54 page booklet. \$39.95.—Voices of New World Parrots is a compendium of exquisite parrot recordings. The authors' hope is that the production of these CD's will aid researchers by presenting a larger sample of the vocalizations made by each species. The selections are lengthy, with up to 5 min per species, and most species are represented by calls given both when perched and in flight. Most species are represented by multiple cuts, especially widely distributed species.

One hundred forty species are included, with a small number of species inevitably missing from the set. Recordings are available—but not included—for the highly endangered Indigo Macaw (*Anodorhynchus leari*) and Little Blue Macaw (*Cyanopsitta spixii*). Information is included in the accompanying booklet on the location of the archive for vocalizations of these species and how to request their use. Recordings were not located for Rufous-fronted Parakeet (*Bolborhynchus ferrugineifrons*), Red-fronted Parrotlet (*Touit costaricensis*), Rose-faced Parrot (*Pionopsitta pulchra*), and Indigo-winged Parrot (*Hapalopsittaca fuertesi*).

Each track includes an announcement with the scientific name of the bird, the common name, and whether the calls are from perched or flying birds, or both (perched/flight or

flight/perched). A small number of recordings include the sounds of begging nestlings and are so identified in the announcement. The selected tracks are clear and generally free of vocalizations of other species. Where other species can be heard, they are generally not identified in either the booklet or on the CD. A few recordings of vulnerable species are from captive birds or aviaries and are identified as such in the booklet.

In addition to providing information on the species and individual recordings, the booklet is packed with information on parrots, research on wild parrots, and the identification of parrots. There is an emphasis on conservation of parrots throughout the booklet. Information on identification includes vocal characteristics as well as flight characteristics, as most views of wild parrots tend to be of birds flying in bad light. Particularly useful is a table of parrot genera, with information on flight and flock characteristics—including undulation, trajectory or rolling, typical height above ground in flight, flock size, and roosting habits. Typical flight silhouettes of birds in each genus are also presented, as well as information on how to record vocalizations of parrots or other wildlife. Taxonomy follows Sibley and Monroe; departures from this standard are noted in the booklet under each species.

For each species, the scientific and common name, International Union for the Conservation of Nature codes for rare and endangered species, and whether the species uses clay licks is also noted. Information on each recording includes whether the birds were perched, flying, or both; the geographic location; catalog information; and the recordist. If known, the number of birds in the flock is provided.

This is an outstanding collection and is recommended as a tool in the identification of parrots.—MARY GUSTAFSON, USGS Patuxent Wildlife Research Center, Laurel, Maryland; e-mail: mary_gustafson@usgs.gov

MASSACHUSETTS BREEDING BIRD ATLAS. By Wayne R. Petersen and W. Roger Meservey (Eds.). Massachusetts Audubon Society, Lincoln, Massachusetts, 2003: 441 pp.,

225 watercolor paintings by John Sill and Barry Van Dusen, 198 range maps, 2 appendices. ISBN: 1558494200. \$60.00 (cloth).—In 1974, following a 1973 pilot study, the Massachusetts Audubon Society, with the cooperation of the Massachusetts Division of Fisheries and Wildlife, and the inspiration of James Baird, launched the first state or province-wide breeding bird atlas (BBA) project in North America. Field work was designed to cover the 1974–1978 breeding seasons, but a 6th year was added, largely to allow time for “blockbusting” (volunteer or paid ornithologists who intensively survey blocks with little or no coverage). Due to personnel changes, various administrative delays, and indecision, results were not published until 2003. Because BBAs are “snapshots in time” of breeding bird distribution in a particular geographical area, they serve as databases against which future atlas data can be compared to determine breeding status trends; thus, the timing of publication is not critical, as long as results eventually are published. Of course, in the interim, the results are not readily available—at least in bound hard copy—for use by land managers and in support of conservation initiatives.

The Massachusetts BBA is a handsome volume, beautifully illustrated, with easy to use range maps, plastic overlays depicting a variety of ecological phenomena, and informative species accounts. The book is wider than long (8.5–10.5 inches; 21.6–26.7 cm), and is divided into sections, the first of which deals with the history of the Massachusetts BBA project. As with all such projects, volunteers played a critical role, with more than 600 involved in data collection and 90 in writing the species accounts. The basic grid was composed of 189, U.S. Geological Survey (USGS) topographical map quadrangles (7.5 minute), subdivided into 6 equal units of approximately 10 square miles (25.9 km²) for a total of 989 blocks within Massachusetts. Because of Massachusetts’ relatively small size and its abundance of bird-oriented people, coverage of virtually every block was possible. During the six field seasons, workers used carefully defined criteria to establish the breeding status of each species encountered within their blocks as “confirmed,” “probable,” and “possible.” Overall, atlas workers document-

ed 198 probable and confirmed species during the count period.

The second section of the book is a discussion of breeding bird distribution in Massachusetts, with subsections on distribution over geologic time, and geographical distribution. The latter includes a discussion of southern species that have expanded their breeding ranges into Massachusetts, other notable recent additions (e.g., Wilson’s Phalarope, *Phalaropus tricolor*), and species that have been introduced by humans. There are also subsections on seasonal distribution, habitat preference, and breeding bird habitats.

The third section deals with Massachusetts’ two major ecoregions and their subdivision into 13 subregions, each of which is described separately (e.g., Boston Basin, Connecticut Valley, Lower Berkshire Hills). An additional feature of the book is a set of eight, heavy, transparent plastic overlays that include towns and counties, an index of USGS quadrangles, ecoregions, major forest types, elevations, major drainages, annual precipitation, and the total number of species tallied in each of the 989 atlas blocks. These overlays, and their discussion in the text, facilitate correlation of breeding bird distribution with a host of ecological factors. Brief sections on atlas methods and criteria, and an explanation of maps and species accounts conclude the text preceding the species accounts.

The bulk of the book (396 pages) is composed of species accounts by multiple authors that provide information on breeding habitat, vocalizations, courtship, nest and eggs, incubation, chicks, fledgling periods, molts, a historical perspective condensed from older literature, and any other interesting or unique characteristics of the species. Each account consists of two facing pages; the left-hand page includes a color illustration of the species and the bulk of the text, and the right-hand page contains the species distribution map that takes up about two-thirds of the page. A key with each map indicates that large-, mid-, and small-sized circles represent confirmed breeding, probable breeding, and possible breeding, respectively. The number of blocks and percentage of total blocks in which a species occurred for each status category is also provided with each map. A brief status assessment of the species is also in-

cluded. Species that are state or federally listed are so noted at the end of the species account. There are few in-text references, which enhances readability.

Most of the species accounts were written by the early 1980s, but the editors updated some accounts, especially where dramatic changes in status had occurred (e.g., Double-crested Cormorant, *Phalacrocorax auritus*). The bibliography has also been updated, with references as recent as 2002 among the 128 presented. A footnote suggests that readers who are interested in further information on status, seasonal distribution, and migratory behavior should consult *Birds of Massachusetts* (Veit and Petersen, Massachusetts Audubon Society, 1993), a book that in many senses is a companion volume to the Massachusetts BBA (many of the BBA maps were first published in *Birds of Massachusetts*, and much of the species account information is complementary rather than overlapping). There is no attempt to estimate species abundances, an artifact, perhaps, of the period when data were collected (early atlas efforts rarely attempted to estimate abundances), and no systematic use of USGS Breeding Bird Survey data.

Appendix 1 contains brief accounts of 20

species that historically nested in Massachusetts or have been discovered nesting there since the atlas period. They include birds such as Manx Shearwater (*Puffinus puffinus*), for which there is a single Massachusetts breeding record (the only recorded breeding in North America) in 1973 on Penikese Island; as well as newer arrivals such as Black Vulture (*Coragyps atratus*), for which there is a single breeding record in 1984; and White-winged Crossbill (*Loxia leucoptera*), confirmed breeding in 2001. Appendix 2 lists plant and animal species mentioned in the text.

Despite the early dates of data collection that precluded many of the modern analytical techniques found in some recent atlases, this is a very welcome addition to the breeding bird atlases of North America. Let us hope that its appearance will stimulate some of the states that have yet to publish their atlas data into doing so. The book is attractive and well edited so that it should appeal to a more general audience than some, more highly technical, atlases. It should be part of every academic library, and should appeal to anyone interested in the distribution of North American birds.—WILLIAM E. DAVIS, JR., Boston University, Boston, Massachusetts; e-mail: wedavis@bu.edu

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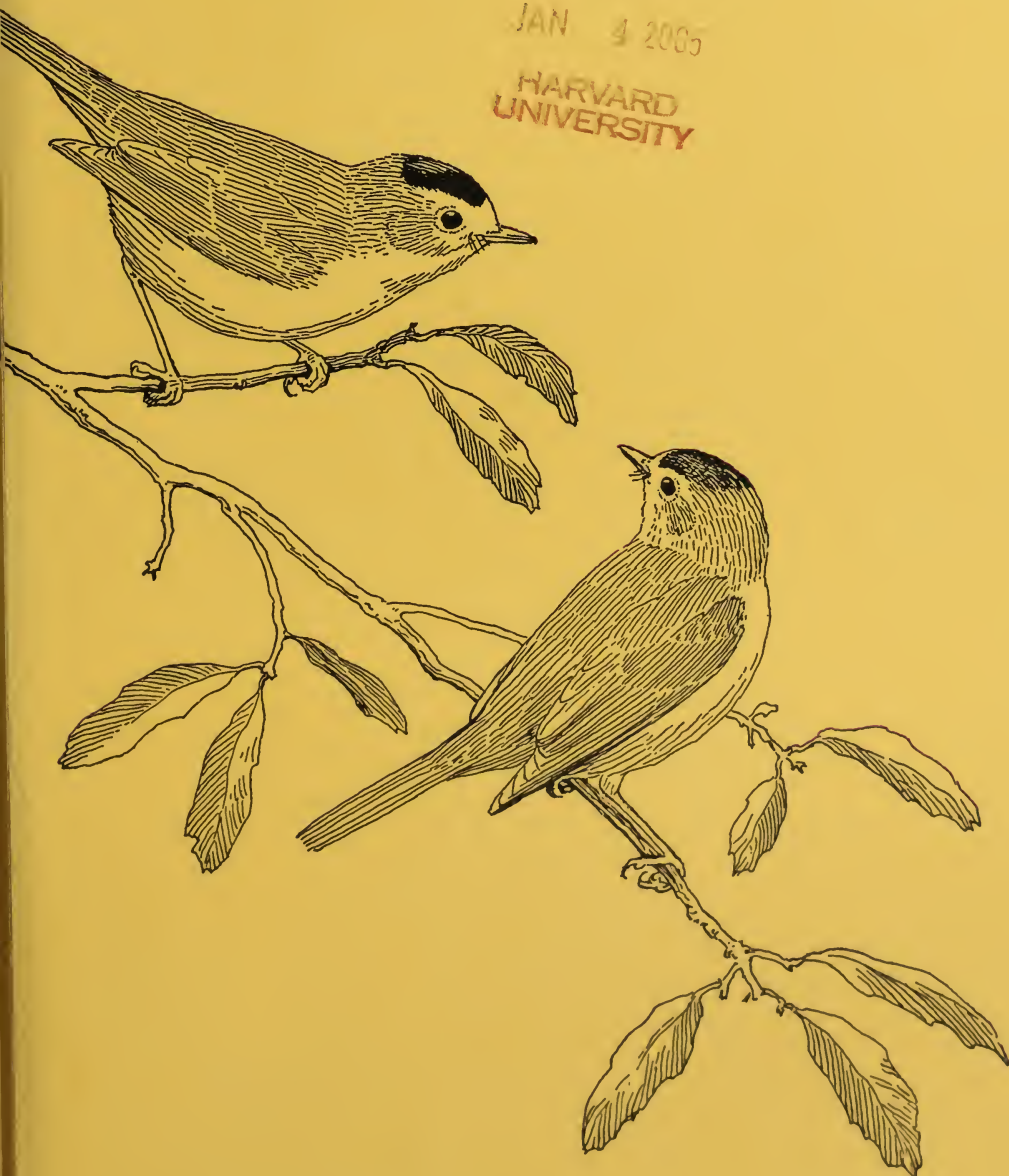
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FRONTISPIECE. Marbled Murrelets (*Brachyramphus marmoratus*) in their preferred nesting habitat in the Pacific Northwest—cool, moist, low-elevation, old-growth forest. Painting by Barry Kent MacKay.

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STAND-SCALE HABITAT ASSOCIATIONS ACROSS A LARGE GEOGRAPHIC REGION OF AN OLD-GROWTH SPECIALIST, THE MARBLED MURRELET

CAROLYN B. MEYER,^{1,3} SHERRI L. MILLER,² AND C. JOHN RALPH²

ABSTRACT.—We used two metrics, occupancy and relative abundance, to study forest stand characteristics believed to be important to a threatened seabird that nests in old-growth forests, the Marbled Murrelet (*Brachyramphus marmoratus*). Occupancy refers to murrelet presence or absence based on observed bird behaviors, while relative abundance refers to categories of low, medium, and high numbers of bird observations per survey in a forest stand. Within the murrelet's nesting range in California and southern Oregon, we measured habitat and climatic variables in all old-growth stands surveyed for murrelets between 1991 and 1997. The two bird metrics produced similar results. In California, murrelets most often occupied, or were abundant in, redwood (*Sequoia sempervirens*) stands with large trees (>100 cm diameter at breast height) located on gentle, low-elevation slopes or on alluvial flats close to streams. In stands of the less flood-tolerant Douglas-fir (*Pseudotsuga menziesii*) in southern Oregon, murrelets most often occupied, or were abundant on, gentle, low-elevation, west-facing slopes that were not close to streams. Murrelets tended to use areas farther from roads. The important climatic requirements for murrelet stands in both states were cool temperatures and high amounts of rainfall. Received 24 November 2003, accepted 10 August 2004.

The Marbled Murrelet (*Brachyramphus marmoratus*) is a species of seabird federally listed as threatened in California, Oregon, and Washington. It usually nests in large trees in old-growth or second-growth forests throughout most of its range, which extends from Alaska to central California (Ralph et al. 1995). Because of logging, its nesting habitat outside of Alaska has been shrinking rapidly (loss of 83–87% in the Pacific Northwest; Booth 1991), and much of what remains is fragmented (Hansen et al. 1991). Some research has been conducted on Marbled Murrelet habitat associations at the landscape and regional scales (Raphael et al. 1995, Meyer et

al. 2002, Meyer and Miller 2002, Miller et al. 2002, Ripple et al. 2003), and a number of local studies (Hamer 1995, Hamer and Nelson 1995, Kuletz et al. 1995, Miller and Ralph 1995) have also addressed nesting habitat characteristics at the stand scale (here, we define a stand as a contiguous patch on the landscape that contains large, old trees; i.e., a patch of old-growth forest). However, no studies have systematically addressed local stand characteristics across a large geographic region. An advantage of a large-scale study is that it is more likely to encompass the full range of stand characteristics, including variation in climate. A comprehensive study in California and southern Oregon is particularly needed because the area is at the southernmost extent of the murrelet's distribution, where murrelets are less abundant and potentially susceptible to extirpation (~5,500 birds in our study area in 2000 compared with 13,100

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birds along a similar length of coastline to the north; Peery et al. 2004; M. H. Huff unpubl. data).

Habitat assessments for birds over large regions often are not possible for several reasons. First, usually many different investigators have conducted the bird surveys using a variety of methods; thus, the data are not comparable across the region. Second, large portions of the study area may not have been surveyed, creating substantial data gaps. Third, some survey methods that give the best habitat information, such as radio-telemetry, are too costly to conduct over large areas and only provide information at a local scale. Fortunately, due to its threatened status and careful coordination among investigators, our Marbled Murrelet study overcomes most of these limitations because the species was surveyed extensively via audio-visual techniques during the 1990s throughout California and southern Oregon by investigators using one common protocol. With the aid of Geographic Information Systems (GIS), we were able to compile all available audio-visual survey data and describe local characteristics of potential nesting habitat across a large region.

One limitation of our approach is that, unlike radio-telemetry methods being used in a few studies in British Columbia (e.g., Bradley and Cooke 2001; F. Huettmann unpubl. data) and California (R. T. Golightly pers. comm.), audio-visual surveys do not identify actual nest sites; rather, they identify potential nest sites based on bird behaviors indicative of nesting. Nevertheless, our extensive dataset of audio-visual surveys (>17,000) can provide complementary information on the distribution and associated habitat characteristics of birds observed inland across a large, bi-state area. Findings based on extensive analyses are currently needed to assist regional recovery and conservation efforts. When published, habitat results from more local nest studies will further enhance the interpretation of extensive studies such as ours by providing more insight regarding the quality and limitations of audio-visual surveys.

In other studies in California and Oregon, many stand-level variables such as mean tree diameter at breast height (dbh), aspect, slope, precipitation, temperature, and distance to nearest stream were of relatively lower signif-

icance compared to broader, landscape variables such as fragmentation and isolation (Meyer et al. 2002, Meyer et al. 2004). Nonetheless, managers are now focusing on these within-stand variables because they contribute additional information about local habitat characteristics important to the biology and conservation of murrelets. Clearly, landscape variables set the stage for the presence and abundance of murrelets, but local variables help clarify stand characteristics preferred by murrelets. For example, we would expect murrelets to more often use stands with the largest trees. Large trees potentially have more branches with platform-like structures available for nesting. Moreover, the nest stands might be in moist, cool areas protected from the wind, such as in low-elevation valley bottoms or on gentle slopes near streams—areas that may be ideal for a coldwater-adapted seabird that nests in the tree canopy (Ralph et al. 1995). To date, there have been no extensive studies to quantify and compare such stand characteristics across such a large area, nor has anyone systematically investigated the importance of precipitation and temperature in stand sites.

It has been suggested that results from presence/absence surveys can be extrapolated to predict population abundance by summing probabilities of use within territories over an area (e.g., Boyce and McDonald 1999). With that approach, only a presence/absence bird metric would be needed for our murrelet study. However, such an extrapolation requires knowledge of the size of the animal's territory. Not only is this unknown for the murrelet, but it is unknown whether Marbled Murrelets behave territorially. Thus, a second metric, relative bird abundance, was needed to complement presence/absence results. In this study we quantified murrelet use of a given stand with both metrics: occupancy (presence/absence) and relative abundance (hereafter, "abundance").

Our main objective was to characterize inland murrelet habitat at the stand level in California and southern Oregon, addressing possible differences in habitat selection between two states that have distinctly different vegetation types and climate. We also compared results using occupancy versus abundance.

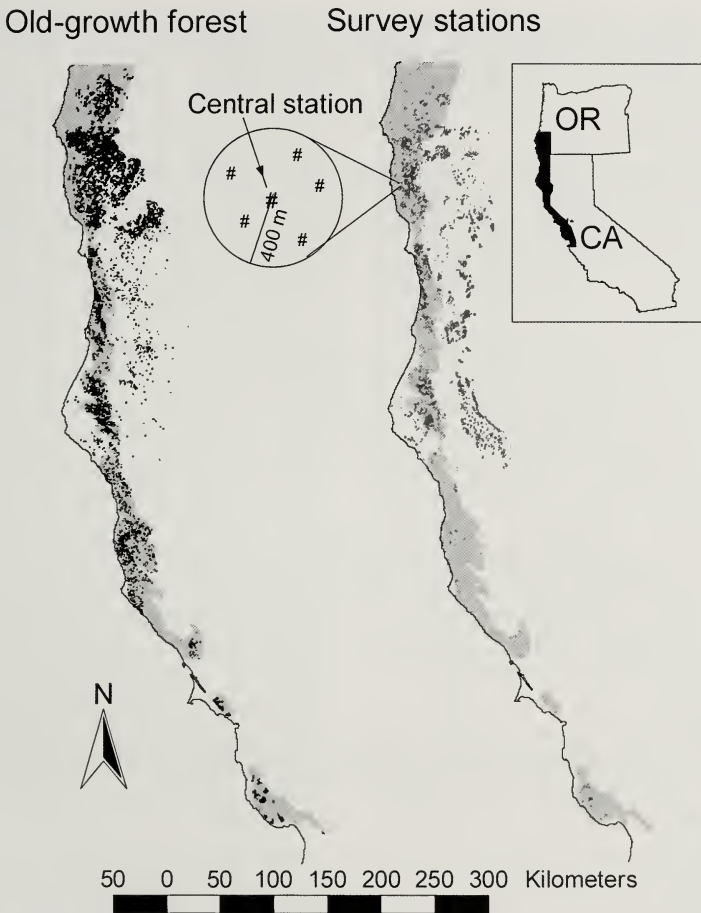


FIG. 1. Marbled Murrelet study area in California and Oregon showing old-growth forest stands (black areas, left map), and locations of all 1991–1997 survey stations (black areas, right map). Based on LANDSAT TM imagery, old-growth stands in California were those with mean tree diameter at breast height (dbh) >91 cm (dominated by redwood) and, in Oregon, mean dbh >77 cm dbh (dominated by Douglas-fir). We limited our surveys to the fog zone (gray shading), as birds were rarely found outside that zone. The inset illustrates one cluster of survey stations; the station at the center represents the “central station,” or the sampling unit in this study. All central stations were >800 m apart. Within a 400-m radius of each central station, we measured stand characteristics, murrelet occupancy (i.e., whether or not we observed “occupancy behavior” in at least one station in the circle), and number of birds per survey (averaged over the stations in the circle).

METHODS

Study area.—The study area encompassed the known nesting range of Marbled Murrelets in California and southern Oregon (based on Meyer 1999 and Meyer et al. 2002). This area extended from Coos Bay, Oregon, south to Monterey Bay, California, and inland up to 40 km from the coast. Because 98% of landscapes occupied by murrelets have been within fog-influenced vegetation zones (Meyer et al. 2002), we studied only those zones (Fig. 1). They included the redwood (*Sequoia sem-*

pervirens) zone in California and the western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) zones in Oregon (Franklin and Dyrness 1973). Douglas-fir (*Pseudotsuga menziesii*) is the dominant tree species in the western hemlock zone and is the species most likely to be used as a nest tree, whereas, in California, redwood trees are used most often (Hamer and Nelson 1995). Based on Meyer et al. (2002), the criteria used to delineate the nesting range were further defined by elevation and distance to key marine

features (see footnote in Table 1). Within this nesting range, average maximum temperature and annual precipitation were 25° C and 203 cm in California and 27° C and 297 cm in southern Oregon, respectively.

Sampling design and murrelet indices of use.—Our study is a retrospective analysis of available survey data, where the sampling design varied from area to area. Surveyors completed 17,145 surveys at 9,326 stations from 15 April to 15 August 1991–1997 (Fig. 1). Forty-six percent of the survey stations were randomly or systematically (in a grid) placed within potential murrelet nesting habitat that contained large platform-like branches; except for a few mature stands surveyed in Oregon, these were mostly found in stands of old-growth forest (hereafter referred to as stands). The remaining survey stations were placed in such habitat near proposed timber sales. The 2-hr surveys began 45 min before dawn according to a standardized protocol for intensive murrelet surveys (Ralph et al. 1994).

Because murrelets rarely used stands outside the fog-influenced vegetation zone, only the 7,616 surveys at 4,158 stations that were within that zone were included in our analyses. From that set of stations, 349 were selected as “central stations” (Fig. 1), each ≥ 800 m apart ($n = 133$ in Oregon and 216 in California). A central station was defined as the one nearest the center of the cluster of stations located within a small (< 50 ha) stand or within a 50-ha section of a large stand (Fig. 1).

To determine occupancy, we classified a central station as either occupied or unoccupied based on murrelet behaviors indicative of nesting. A central station was considered occupied if any of the following behaviors were observed at any survey station within a 400-m radius (50 ha) of the central station: a bird flew below the canopy, circled above the canopy, landed in the canopy, was stationary in a tree, or broken eggshells were found (Ralph et al. 1994). Central stations with no murrelets observed or heard at any station within a 400-m radius were considered “unoccupied.” We deleted from the analysis any central stations where birds were seen or heard at a station within the 400-m radius, but occupancy status could not be verified (i.e., stations had birds “present” but no occupying behaviors were

observed). To ensure 91% confidence that the remaining unoccupied areas with no birds seen or heard did not have murrelets “present” in the surveyed year, at least four surveys must have been conducted in 1 year within the 400-m radius area (based on an analysis in Evans Mack et al. 2003, Appendix A, p. 40) before the central station was assigned “unoccupied” status (otherwise it was deleted from the analysis). This confidence rate does not consider that the status of a site may change between years. Most of our stands were not surveyed in more than 1 year because the survey protocol initially did not require it. During the later years of this study, there was a change in the recommended number of surveys and years. To retain our ample data collected during the early years of our study, we used the early survey protocol and accepted that some of the unexplained variance in our models would be due to some unoccupied central stations actually being occupied in years they were not surveyed. Henceforth, the use of the term “station” in this paper will refer to the central station and its associated stand characteristics within the 400-m radius circle surrounding the central station (Fig. 1).

Our index of abundance was the total number of standardized bird detections observed during each survey averaged over all surveys conducted within 400 m of the central station. Each visual or auditory observation of a single bird or group of birds was considered one “detection.” In each state, the total number of detections was standardized by applying a multiplier to adjust for seasonal variations over time. On average, detections peak in July in both California (O'Donnell et al. 1995) and Oregon (Jodice and Collopy 2000). For the 12 consecutive 10-day periods starting with 15 April, the multipliers were 1.14, 1.81, 1.22, 1.36, 1.12, 1.40, 1.29, 0.93, 0.81, 0.59, 0.61, and 1.14. These multipliers are the ratio of the mean number of detections for the entire survey season divided by the mean for each 10-day period obtained from pooled surveys at three long-term (1989–1995) monitoring sites in northern California (Miller and Ralph 1995).

On average, six surveys contributed to the final mean number of murrelet detections assigned to a central station. Because differenc-

TABLE 1. Means (\pm SD) of old-growth forest variables at stations occupied or unoccupied by Marbled Murrelets and at those with low, medium, or high murrelet abundance within the species' nesting range^a in California and Oregon. Compared with unoccupied stations, occupied stations contained larger trees (dbh); were located on cooler, drier, lower-elevation sites; and had gentler slopes closer to streams. When compared with stations with low (<2) or medium (2–15) murrelet abundance, stations in California with the highest abundance (>15 detections per survey) were located in cooler, lower-elevation sites and those with gentler slopes closer to roads. In Oregon, occupied stations were at cool, low elevations with more west-facing aspects, but no variables differed significantly across abundance categories. Bold-faced values significant at $P < 0.05$ (Kruskal-Wallis test unless otherwise noted).

Variable	Occupancy			Abundance			P
	Unoccupied	Occupied	P	Low	Medium	High	
California	n = 85	n = 131		n = 21	n = 62	n = 48	
Mean tree dbh (cm) ^b	70 (49)	135 (38)	<0.001	124 (41)	138 (37)	138 (37)	0.25
Elevation (m)	423 (214)	235 (152)	<0.001	291 (148)	272 (157)	162 (117)	<0.001
Slope (°)	12 (7)	8 (7)	<0.001	10 (7)	10 (7)	4 (4)	<0.001
Distance to stream (m)	359 (291)	291 (289)	0.034	312 (350)	293 (263)	279 (299)	0.89
East-facing (sine aspect) ^c	-0.04 (0.77)	-0.04 (0.72)	0.94	-0.17 (75)	-0.02 (0.70)	-0.01 (0.74)	0.62
North-facing (cosine aspect)	0.01 (0.65)	0.01 (0.70)	1.00	0.01 (0.68)	0.01 (0.73)	0.00 (0.69)	0.99
Distance to road (m)	288 (321)	295 (375)	0.58	328 (305)	375 (409)	177 (330)	<0.001
Maximum temperature (°C)	26 (2)	24 (2)	<0.001	25 (2)	24 (2)	23 (2)	0.011
Annual precipitation (cm)	214 (44)	195 (35)	0.010	192 (31)	198 (34)	194 (39)	0.48
Southern Oregon	n = 62	n = 71		n = 27	n = 39	n = 5	
Elevation (m)	570 (241)	402 (187)	<0.001	413 (157)	396 (212)	389 (156)	0.79
Slope (°)	13 (6)	14 (7)	0.35	15 (9)	15 (6)	10 (6)	0.26
Distance to stream (m)	493 (310)	472 (404)	0.27	549 (401)	394 (379)	667 (550)	0.090
Distance to road (m)	415 (337)	426 (433)	0.74	380 (388)	448 (442)	505 (645)	0.83
East-facing (sine aspect)	-0.01 (0.70)	-0.33 (0.65)	0.009	-0.34 (0.64)	-0.35 (0.65)	-0.07 (0.85)	0.76
North-facing (cosine aspect)	0.08 (0.72)	0.15 (0.68)	0.58	0.08 (0.72)	0.16 (0.69)	0.19 (0.67)	0.42
Maximum temperature (°C)	27 (2)	26 (2)	0.045	26 (2)	27 (2)	26 (1)	0.86
Annual precipitation (cm)	303 (68)	291 (40)	0.22 ^d	296 (46)	288 (37)	286 (40)	0.90

^a In California, murrelet nesting range was defined as that part of the fog zone occurring at ≤ 880 m elevation, ≤ 42 km from marine areas with high spring chlorophyll, and ≤ 50 km from submarine canyons. In Oregon, nesting range was that part of the fog zone ≤ 918 m elevation and ≤ 38.5 km from marine areas with high summer chlorophyll. Only a few occupied stations were found outside these areas (Meyer 1999).

^b Dbh values were available only from the northern border of California to Point Reyes National Seashore, yielding samples sizes (n) of 20, 60, and 42 for low-, medium-, and high-abundance stations, respectively.

^c Some slopes in California were 0° (no aspect); thus, aspect $n = 82$ for unoccupied and 118 for occupied stations.

^d P -value for t -test with unequal variances (Kruskal-Wallis, $P = 0.034$).

es between observers, daily survey conditions, or daily murrelet activity can cause murrelet survey results to vary, even when averaged over six surveys (Jodice et al. 2001), we assigned means to four levels of detections: zero, low (<2), medium (2–15), and high (>15), and used the categories, rather than the actual means, in our analyses. Such category boundaries are useful for showing differences in landscape variables (Meyer et al. 2002).

We assumed that the abundance metric was positively correlated to the number of nesting birds in a stand or section. To what extent this is true is unclear. The number of birds detected may be biased by the size of the forest canopy opening (Rodway and Regehr 2000), skill of the observer, weather, the flight path of the birds from the ocean to the nest site, or by the high variability in number of birds detected during each survey at a station (Jodice and Collopy 2000, Buckland et al. 2001, Jodice et al. 2001). Although the occupancy metric also can be biased by these factors, such problems probably would be associated with the abundance metric more than with the more robust occupancy metric (Rodway and Regehr 2000). Thus, we compared the interpretation of the results of the two methods to assess whether such biases might have occurred.

Forest stand variables.—We recorded elevation, slope, aspect (using 90-m digital elevation models), and distance to nearest stream or major road (identified with 1:100,000 digital line graphs) from each central station. To create linear variables from a circular distribution, aspect was divided into an east-west component using the sine of the aspect and a north-south component using the cosine of the aspect (in radians). Sine and cosine values range from 1 to -1, where positive values represent eastern and northern aspects and negative values represent western and southern aspects (Briggle and Prather 2003).

The annual precipitation and maximum temperature for the summer, averaged over the survey period (1991–1997), were measured at each station using PRISM (Parameter-Elevation Regressions on Independent Slopes Model) at a 4-ha resolution (Spatial Climate Analysis Service, Oregon State University, <http://www.ocs.orst.edu/prism>). This analytical model interpolates station data for monthly and annual climate, accounting for orographic,

coastal, and hillslope exposure effects, and distributes such data onto a regular grid across the landscape (Daly et al. 2002).

The estimated mean dbh of canopy conifers in each stand was obtained for each station in northern California only (Point Reyes National Seashore to northern border) from a GIS database in ARC/INFO developed by the California Timberland Task Force (1993). Estimates of mean tree dbh for each stand on a 4-ha resolution GIS map were derived using remote sensing techniques (spectral signatures compared to ground observations) from LANDSAT Thematic Mapper (TM) imagery. Unfortunately, the expected accuracy of the mean dbh for each stand in our study was not available. However, this remote satellite approach was effective in identifying the size class >91 cm dbh (82.8% accuracy; California Timberland Task Force 1993), and the dbh datasets appeared reasonable given our knowledge of some areas. The quadratic mean diameter at breast height (QMD) was used to estimate the mean stand dbh. QMD is a measure applicable to the Marbled Murrelet because it emphasizes the dbh of large trees. The formula weights dbh by the percent tree cover (cover) contributed by that size tree:

$$QMD = \frac{\sum_{i=1}^n dbh_i^2 \cdot cover_i}{\sum_{i=1}^n cover_i},$$

where i is the i^{th} class of n dbh classes.

Statistical analyses.—We used either non-parametric Kruskal-Wallis tests or t -tests with unequal variances ($\alpha = 0.05$; Sokal and Rohlf 1981) to detect differences in mean ranks or means of forest stand variables (1) between occupied and unoccupied stations, and (2) among the abundance categories of occupied stations. Both tests identified almost the same set of variables as significant (one exception, shown in Table 1), even though many variables had highly skewed distributions (thus, the Kruskal-Wallis test was used for most comparisons). To evaluate whether abundance provided useful information beyond that provided by occupancy, stations with zero abundance (unoccupied stations already used in the occupancy analysis) were not included in the comparison of abundance categories.

We used multiple logistic regression to predict murrelet use and assess the effect of habitat variables in combination. Binary logistic regression was used to relate occupancy to habitat variables. Ordinal logistic regression was used to relate murrelet abundance (zero to high categories) to the variables. Ordinal logistic regression creates three regressions with parallel slopes but different intercepts, where each category is contrasted with the highest abundance category. For the ordinal logistic regressions, we added the zero category to the other three abundance categories to include the full range of abundance levels.

For each regression analysis, we developed 15 candidate *a priori* model combinations that were the most biologically meaningful. We calculated Akaike's Information Criterion (AIC_c , corrected for sample size) for each model in SAS (SAS Institute, Inc. 1990). The models were ranked by ΔAIC_c , and the models with $\Delta AIC_c < 2$ (which had the highest Akaike weights) were selected as the best models (Burnham and Anderson 2002). Multicollinearity was not a problem (Neter et al. 1989) because no two variables were highly correlated (all $r < 0.6$); models also met the assumption of linearity (Neter et al. 1989).

The predictability of the logistic regressions was assessed by comparing Somers' d among the models. To calculate Somers' d , all possible pairs of stations are compared, where each in the pair is in a different category. For example, in the occupancy models, the proportion of such pairs in which the occupied station has a higher predicted probability of occupancy than the unoccupied station is recorded as the proportion of concordant pairs. This proportion is adjusted to range from -1 to 1 . Zero is no correlation and 1 or -1 is perfect positive or negative correlation between observed and predicted occupancy (Harrell 2001).

RESULTS

Tree size.—In California, dbh was greater in occupied stands than in unoccupied stands (dbh data were unavailable for Oregon; Table 1). Only 54% of stations in the fog zone with mean dbh between 100 and 140 cm were occupied, whereas almost all (91%) stations with larger tree sizes were occupied (Fig. 2A). The majority (79%) of stations in the fog zone

with mean tree dbh below 100 cm were not occupied. Mean dbh was much larger inside than outside of the fog zone (where occupied behaviors suggestive of nesting generally do not occur; Fig. 2B). At the occupied stations, dbh did not significantly differ across murrelet abundance categories (Table 1).

Elevation.—Occupied stations averaged 188 and 168 m lower in elevation than unoccupied stations in California and southern Oregon, respectively (Table 1). Elevation was lower at high-abundance stations in California ($P < 0.001$) but not in Oregon ($P = 0.79$; Table 1). The difference in elevation between stations with zero and high abundance (>15 detections per survey) was significant in both states (Kruskal-Wallis, $P < 0.001$).

Location in drainage.—Slope, aspect, and distance to nearest stream provide insight into locations within a drainage potentially used for nesting. In southern Oregon, location in the drainage did not differ between occupied and unoccupied stations, except that occupied stations were more west-facing than unoccupied stations (Table 1). In contrast, slope in California differed between occupied and unoccupied stands and across the three abundance categories; unoccupied stations had slopes (12°) that were three times steeper than the slopes of high-abundance stations (4°). Although occupied stations were significantly closer to streams (291 m) than unoccupied stations (359 m) in California, there was no difference among abundance categories in distance to stream (Table 1). In contrast to Oregon, aspect in California did not differ between occupied or abundance categories.

Distance to roads.—California stations with high bird abundance were significantly closer to roads than were stations with medium or low abundance, but distance to roads did not differ between occupancy categories. Road distance was not significantly related to occupancy or abundance in Oregon (Table 1).

Climate.—In California, occupied and high-abundance stations had cooler maximum summer temperatures than unoccupied stations (Table 1). Temperatures were 2°C cooler at occupied stations, and 3°C cooler at high-abundance stations. In southern Oregon, occupied stations were significantly cooler than unoccupied stations but temperatures did not differ among abundance categories. Precipitation

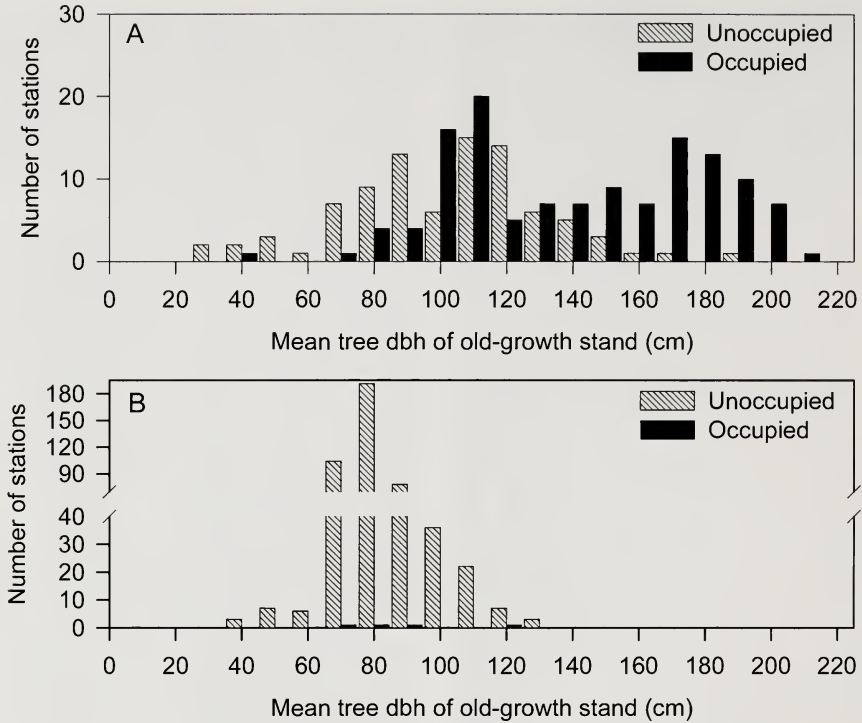


FIG. 2. From 1991 to 1997 in California, occupancy by Marbled Murrelets was highest in old-growth stands with a large mean tree diameter at breast height (dbh) of canopy trees, especially in the fog zone. A = inside fog zone, B = outside fog zone.

tation results were less clear. Precipitation was not significantly related to either occupancy or abundance in southern Oregon or to abundance in California. However, occupied stations in California were significantly drier than unoccupied stations.

Variables in combination.—The best binary logistic regression model in California (predicting occupancy) included tree size, maximum temperature, elevation, and precipitation (first model; Table 2). Based on Akaike weights, this model had about twice the support for being the best model compared with the two next-best combinations of variables (evidence ratios of the weights between two compared models ranged from 1.8 to 2.1); these models had the same variables but also included slope (second model) or distance to road (third model). All three models ($\Delta AIC_c < 2$; Table 2) indicate murrelets occupied stands on low-elevation, cool, moist, gentle slopes with large trees in areas farther from roads.

The best ordinal logistic regression (abun-

dance) in California also included dbh, temperature, elevation, precipitation, and slope (first model; Table 3). Based on the evidence ratio, this model had 2.7 \times the support of the next-best model. Similar to the occupancy models, these models indicate that murrelets were most abundant in low elevation, cool, moist stands with gentle slopes and large trees. The predictability (Somers' *d*) of the occupancy models was higher than that of the abundance models (Tables 2 and 3).

The best binary logistic regression model for southern Oregon included elevation, east-west aspect, precipitation, and distance to stream, indicating that murrelets occupied sites that were often on low-elevation, high-precipitation, west-facing slopes far from streams (first model; Table 2). The next three best models of occupancy ($\Delta AIC_c < 2$) had about one-third less support for being the best model (Table 2).

The first four ordinal logistic regression models (abundance) for Oregon included elevation, east-west aspect, distance to stream, or

TABLE 2. The top three (where $\Delta AIC_c < 2$) of the five best candidate binary logistic regression models—ranked in order of ΔAIC_c —indicate that stands occupied by Marbled Murrelets in California had larger mean tree dbh, lower elevations, cooler temperatures, greater precipitation, flatter slopes, and were farther from roads ($n = 207$) than unoccupied stands. In Oregon, the top four models ($\Delta AIC_c < 2$) indicate that occupied stands were on west-facing aspects at lower elevations with greater precipitation and were farther from streams ($n = 133$) than unoccupied stands. K = number of parameters.

Model	K	AIC_c	ΔAIC_c	Akaike weight	Somers' d
California					
Dbh, elevation, temperature, precipitation	5	143.97	0.00	0.334	0.866
Dbh, elevation, temperature, precipitation, slope	6	145.08	1.11	0.191	0.870
Dbh, elevation, temperature, precipitation, road	6	145.42	1.45	0.162	0.868
Dbh, elevation, temperature, precipitation, road, slope	7	146.34	2.37	0.102	0.872
Dbh, elevation, temperature, precipitation, stream	5	147.19	3.22	0.067	0.868
Southern Oregon					
Elevation, east, precipitation, stream	5	162.92	0.00	0.230	0.528
Elevation, east, precipitation	4	163.69	0.77	0.156	0.502
Elevation, east	3	163.90	0.98	0.141	0.486
Elevation, east, stream	4	163.90	0.98	0.141	0.498
Elevation, east, north, precipitation	5	165.45	2.53	0.065	0.498

precipitation in various combinations; Akaike weight did not strongly separate these models (Table 3). The fifth-best model, which included distance to road, had a lower Akaike weight but still had $\Delta AIC_c < 2$; thus, it is also a comparatively good model. Overall, the Oregon models had lower predictability than the California models (Somers' d ; Tables 2 and 3).

DISCUSSION

Assuming that occupied stands are used for nesting, our study suggests that Marbled Murrelets prefer to nest in cool, moist, low-elevation stands of old-growth forest that contain the largest trees. Estimates of murrelet abundance within occupied stands added additional information on habitat requirements, often when the relationship between habitat

TABLE 3. The top model ($\Delta AIC_c < 2$) of the best five candidate ordinal logistic regression models—ranked in order of increasing ΔAIC_c —indicates that Marbled Murrelets in California were most abundant in stands with large trees at lower elevations, cooler temperatures, greater precipitation, and flatter slopes ($n = 207$). For Oregon, the top five models ($\Delta AIC_c < 2$) indicate that murrelets were most abundant in stands with west-facing aspects, lower elevations, greater precipitation, and which were farther from streams and roads than sites where murrelets were less abundant ($n = 133$). K = number of parameters.

Model	K	AIC_c	ΔAIC_c	Akaike weight	Somers' d
California					
Dbh, elevation, temperature, precipitation, slope	8	384.14	0.00	0.469	0.730
Dbh, elevation, temperature, precipitation, slope, road	9	386.15	2.01	0.172	0.730
Dbh, elevation, temperature, precipitation, slope, stream	9	386.32	2.18	0.157	0.730
Dbh, elevation, temperature, slope, stream	8	387.19	3.05	0.102	0.722
Dbh, elevation, temperature, precipitation, slope, stream, road	10	388.36	4.22	0.057	0.730
Southern Oregon					
Elevation, east	5	296.80	0.00	0.196	0.366
Elevation, east, precipitation	6	297.33	0.53	0.150	0.380
Elevation, east, stream	6	297.76	0.96	0.121	0.372
Elevation, east, precipitation, stream	7	297.77	0.97	0.121	0.389
Elevation, east, road	6	298.07	1.27	0.104	0.362

variables and occupancy (presence/absence) was strong (Table 1). Overall, the interpretation of the results was similar, whether using the occupancy or abundance metric (Tables 2 and 3).

Tree size.—As expected based on previous research, murrelets in California most consistently used stands with the largest trees. As tree size decreased, stands were often unoccupied, especially those with mean dbh ≤ 100 cm. Other studies in Oregon, Washington, and Alaska have shown similar trends (Rodway et al. 1993, Grenier and Nelson 1995, Hamer 1995, Kuletz et al. 1995). Larger trees often have more potential nest platforms than smaller trees (Hamer 1995, Naslund et al. 1995), although, as Hamer (1995) postulated, epiphytes on some smaller trees can effectively thicken branches, thus providing platforms for nest sites.

Slope position.—As predicted, murrelets in California most often used cool, moist, forests on gentle, low-elevation slopes near the bottom of drainages where the largest trees grow. Similarly, birds in southern Oregon used cooler and moister low-elevation areas, but not as low as in California. Unlike California murrelets, the Oregon birds tended to use west-facing slopes farther from streams, and the steepness of the slope was not important. The difference in slope position and distance from stream may be due to differences in dominant tree species used for nests between the two states. Unlike redwood trees, which grow largest along alluvial flats in California (Agee 1993), coastal Douglas-fir in Oregon is not adapted to flooding and does not grow well adjacent to streams (Stone and Vasey 1968). Thus, in Oregon, the best nest platforms may be in the largest Douglas-fir trees, which are farther from streams and higher on the hillside.

Data from other studies support our finding that forests with mostly flood-intolerant tree species may have more murrelet occupancy higher on the hillside—in contrast to forests with flood-tolerant tree species that may have the best nesting sites at lower elevation, on gentler slopes, and in flood-prone areas. In central Oregon just north of our study area, where the more flood-intolerant Douglas-fir was the dominant tree used by murrelets, occupied stands were mostly on the gentler

slopes of middle and upper portions of hill-sides (Grenier and Nelson 1995). In a Washington study that included areas dominated by flood-intolerant Douglas-fir trees, as well as other tree species used by murrelets that were more tolerant of flooding [western red cedar (*Thuja plicata*) and Sitka spruce; Duddles and Fitzgerald 1998], the probability of murrelet occupancy of a stand was highest on lower to middle portions of the hillside, and increased as slope increased (Hamer 1995). A study of 45 actual nest sites across the Pacific Northwest showed that, on average, nests were located on the lowest slopes in California, on the highest in Oregon, and on intermediate slope positions in Washington (Hamer and Nelson 1995), corresponding to the proportion of the dominant tree species that are flood-tolerant. Although there may have been a bias because areas were not randomly searched to locate nests, the trend in that nest study is suggestive.

One study does not support our finding that areas with flood-tolerant tree species have more murrelet use near the bottom of drainages. In a recent study of 157 actual nest sites in British Columbia forests near Desolation and Clayoquot sounds, murrelets avoided flat areas (F. Huettmann unpubl. data) even though the forests had many flood-tolerant species. It is difficult to compare our study area with British Columbia because slopes in our area are not as steep and the large avalanche chutes that are commonly found in British Columbia do not occur in Oregon and California. More research is needed to evaluate the relationships between tree size and number of potential nesting platforms in relation to position on slope and tree tolerance to flooding.

Elevation.—The apparent preference of Marbled Murrelets for nesting in relatively low-elevation sites (not necessarily at the bottom of valleys) appears to be fairly consistent across its range from Alaska to California (Rodway et al. 1993, Burger 1995, Grenier and Nelson 1995, Hamer 1995, Kuletz et al. 1995, Miller and Ralph 1995, Manley 1999). One might argue that lower-elevation sites tend to be closer to the coast, and, thus, increased use could be due to closer proximity to marine habitat. However, studies in California and southern Oregon have shown that low elevation is important even when prox-

imity to marine habitat has been taken into account (Meyer and Miller 2002, Meyer et al. 2002).

For studies in which low elevation was found to be important to murrelet use, only Rodway et al. (1993), Miller and Ralph (1995), and this study clearly demonstrate that the elevation effect is related to slope position, with murrelets more often occupying stands at the bottom of local major drainages rather than occupying ridge tops. On a more regional scale, murrelets also may be responding to less favorable vegetation conditions that occur as elevation increases (Burger 1995, Hamer 1995). For example, in Washington and British Columbia, high-elevation trees such as silver fir (*Abies amabilis*) and mountain hemlock (*Tsuga mertensiana*) may be smaller and have fewer platform branches than trees that occur at low elevations—such as western hemlock, western red cedar, Douglas-fir, and Sitka spruce (Rodway et al. 1993, Hamer 1995). However, murrelets readily nested in high-elevation (>800 m) forests composed of mountain hemlock and yellow cedar (*Chamaecyparis nootkatensis*) in British Columbia (Manley 1999, Bradley 2002), even though they marginally preferred forests at elevations of <800 m (F. Huettmann unpubl. data). Although they may prefer lower elevations, murrelets readily use high-elevation forests.

Murrelets probably are responding to factors correlated to elevation, rather than to elevation itself. High elevations along ridge tops may be used less because branch growth needed to develop nest platforms may be less optimal (Daniel 1942), or wind damage may be higher. Also, fog—which provides cooler conditions for nesting birds and obscures a predator's view of nests—burns off more quickly on ridge tops.

Climate.—As predicted, murrelets used relatively cool forest stands with high amounts of precipitation (mostly rain). Although we hypothesized that such areas would be used by a coldwater-adapted seabird (Ralph et al. 1995), more use could also result if cool, moist environments promote more epiphyte growth on branches (i.e., suitable nest sites). In California, birds often occupied drier areas (Table 1), but once tree size was taken into account, the areas of greater precipitation had greater occupancy. In regard to temperature,

other studies have shown that murrelets avoid warm areas, even where suitable nest sites are available (Dillingham et al. 1995, Hunter et al. 1998). Our study is the first to show that, even within the fog zone, murrelets appear to prefer moist areas with the coolest temperatures. Laboratory studies on the physiological tolerances of murrelets are needed to help validate this apparent preference.

Distance to roads.—When elevation was taken into account (Tables 2 and 3), regression analyses showed that sites used by murrelets were often farther from roads than sites without murrelets. We obtained this result even though birds might be detected more easily at survey stations near roads. In a previous study, wherein the level of fragmentation in old-growth forest was taken into account, murrelets were most abundant in sites farther from roads (Meyer et al. 2002). These results suggest that human disturbance and noise along roads may reduce murrelet use of an area.

Potential biases in indices based on audio-visual surveys.—We used occupancy as an index to murrelet nesting, and abundance as an index to number of nesting murrelets in a stand. These metrics may be poor proxies for nesting if they are biased by survey station placement. Rodway and Regehr (2000) showed that audio-visual survey sites near streams often have larger canopy openings than sites farther from streams, making it possible to detect more birds and more below-canopy flight or circling, two major behaviors used to classify a site as occupied. Consequently, detections may be upwardly biased in low-elevation valley bottoms with gentle slopes, even when the birds have no preference for using such areas. Moreover, murrelet abundance may be inflated if the birds use streams as travel corridors (Rodway and Regehr 2000). We detected higher occupancy and abundance in valley bottoms in California, possibly due to this bias; however, results in Oregon did not show the same trend. The lower predictability of our abundance models suggests that such biases and the high daily variability in number of detections made it more difficult to detect a significant relationship between abundance and habitat variables than between occupancy and the same variables. More actual nest sites need to be iden-

tified in our study area using unbiased techniques, so that our results for occupancy and abundance, both of which are affected by detectability, can be compared with results of other studies.

In summary, our results suggest that recovery efforts for murrelets in our study area should focus on protecting cool, moist, low-elevation stands of old-growth forest with the largest-dbh trees, and that these areas should be far from roads. In California, redwood stands along alluvial flats adjacent to streams should be given high priority, and, in southern Oregon, the low-elevation Douglas-fir stands higher on hillsides should be given priority. This information, along with landscape and regional-level results from other studies, can help managers prioritize recovery efforts. More research is needed to establish the link between occupancy, abundance, and nest density to verify our conclusions.

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NESTING BIOLOGY OF THREE GRASSLAND PASSERINES IN THE NORTHERN TALLGRASS PRAIRIE

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ABSTRACT.—Basic nesting information on grassland passerines is needed for improving grassland bird management. Among the information needs are (1) the suitability of nesting habitat, (2) periods during the breeding season in which birds are most vulnerable to disturbances, and (3) how to fit grasslands into a prioritization scheme for conservation. Comparisons of nesting parameters among grassland species will help identify important management considerations. We describe and compare nest-site characteristics, nesting phenology, clutch size, hatching and fledging success, and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) for three grassland passerine species nesting in tallgrass prairie of northwestern Minnesota and southeastern North Dakota. During 1998–2002, we found 793 Clay-colored Sparrow (*Spizella pallida*), 687 Savannah Sparrow (*Passerculus sandwichensis*), and 315 Bobolink (*Dolichonyx oryzivorus*) nests. These species differed in many aspects of their breeding ecology. Clay-colored and Savannah sparrows initiated their nests almost 2 weeks earlier than Bobolinks, with peak nesting occurring in June. Clutch size was lower (3.77 ± 0.03 SE) for Clay-colored Sparrows than Savannah Sparrows (4.13 ± 0.05) and Bobolinks (5.25 ± 0.08). The number of host eggs hatched per nest was higher in Bobolinks (3.46 ± 0.20) than in Clay-colored Sparrows (2.52 ± 0.09) and Savannah Sparrows (2.41 ± 0.11), but the number of young fledged per Bobolink nest (1.97) was similar to that of Savannah Sparrows (2.01). Clay-colored Sparrows fledged only 1.35 host young per nest. Mayfield nest success was higher for Savannah Sparrows (31.4%) than for Clay-colored Sparrows (27.4%) or Bobolinks (20.7%). The main cause of nest failure was nest predation: predation in Clay-colored Sparrows (47.9%) was higher than in Savannah Sparrows (33.5%) but similar to Bobolinks (41.8%). Brood parasitism was lower in Clay-colored Sparrows (5.1%) than in Bobolinks (10.8%), and intermediate (6.7%) in Savannah Sparrows. Compared with most other studies, grassland bird nests in our study area were more successful and less frequently parasitized; thus, northwestern Minnesota and southeastern North Dakota appear to provide important breeding habitat for grassland birds. Received 5 August 2003, accepted 29 July 2004.

Even though many species of grassland birds have experienced sharp population declines in the last four decades (Peterjohn and Sauer 1999), we still know little about the natural histories of most grassland-nesting bird species. To better understand these population declines and to develop effective management guidelines, we need basic information on the natural history of the species, including knowledge of nesting ecology. Specifically, more information is needed on (1) nest-site characteristics—to determine whether a specific habitat is suitable for nesting of a given

species, (2) the timing of nesting and changes in breeding performance (clutch size and nest success) over the breeding season—to determine the periods in which grassland birds are most vulnerable to disturbances such as haying, and (3) general breeding performance of a species [including clutch size, hatching and fledging success, and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*)]—to prioritize prairie patches in conservation plans. A comparison of these parameters among species will indicate which should be considered in managing for a given species and whether species are likely to respond similarly to certain management actions. Such comparisons might also suggest whether indicator species would be valid tools for managing grassland birds.

In this paper, we describe and compare breeding parameters of three grassland species nesting in some of the largest patches of native tallgrass prairie remaining in Minnesota and North Dakota: Clay-colored Sparrow (*Spizella pallida*), Savannah Sparrow (*Passerculus sandwichensis*), and Bobolink (*Dolicho-*

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TABLE 1. Number (n) and combined area of study plots, and number of nests found for Clay-colored Sparrows (CCSP), Savannah Sparrows (SAVS), and Bobolinks (BOBO) in tallgrass prairie in Minnesota (Crookston and Glyndon regions) and North Dakota (Sheyenne National Grassland), 1998–2002.

Region	Year	n	Area (ha)	CCSP ^a	SAVS	BOBO
Crookston	1998	10	101.94	22	49	23
	1999	12	124.72	86	150	27
	2000	11	121.37	32	143	24
	2001	12	120.58	119	135	69
	2002	3	40.52	13	29	11
Glyndon	1998	11	115.06	75	21	25
	1999	9	95.33	119	25	20
	2000	9	95.33	93	25	18
	2001	10	104.23	63	20	31
Sheyenne	1999	9	101.13	55	27	9
	2000	8	99.86	62	44	22
	2001	9	113.95	54	19	36

^a Number of nests found differs from that given in the following tables because not all nests could be used for each analysis.

nyx oryzivorus). During 1966–1999, these species declined in abundance across North America (Sauer et al. 2003).

The breeding ecology of our focal species is summarized in Knapton (1994) and Dechant et al. (2003a) for Clay-colored Sparrows; in Wheelwright and Rising (1993) and Swanson (2003) for Savannah Sparrows; and in Martin and Gavin (1995), Swanson (1996), and Dechant et al. (2003b) for Bobolinks. Most studies in these reviews had been conducted in portions of the species' ranges different from our study area or on island populations (for Savannah Sparrows; Dixon 1978, Wheelwright and Mauk 1998), or they were based on relatively small sample sizes (Lein 1968, Koford 1999). Nesting data collected in relatively large and intact grassland habitats are expected to reflect higher breeding success and lower brood parasitism by Brown-headed Cowbirds than documented in other regions (Herkert et al. 2003). Data from such "high-quality" areas, therefore, can serve as a baseline for comparisons with other habitats. Such data are often lacking because large, intact patches of prairie are rare, and sample sizes are low because nests can be difficult to locate (Winter et al. 2003). The large number of nests ($n = 1,795$) that we found over a large regional (three regions approximately 50 km apart) and temporal (1998–2002) scale in some of the largest remnants of native tallgrass prairie likely provide reliable baseline data for future prioritization schemes.

METHODS

Study area.—We searched for grassland bird nests in 33 permanent study plots that were established in patches of native prairie located in three regions of the northern tallgrass prairie: the Crookston and Glyndon regions in northwestern Minnesota (1998–2002), and the Sheyenne region at Sheyenne National Grassland in southeastern North Dakota (1999–2001; Table 1). The Crookston and Sheyenne regions were located about 50 km north and about 50 km southwest, respectively, from the centrally located Glyndon region. In 2002, our study was limited to three plots in the Crookston region. All prairie patches were on U.S. Fish and Wildlife Service, U.S. Forest Service, State of Minnesota, or Nature Conservancy lands (Winter et al. 2001). Prairies in the Crookston and Glyndon regions were managed with prescribed burning, whereas Sheyenne prairies were managed with rotational grazing. Because management regime was confounded with region, we could not differentiate between management and regional effects, and therefore did not address management questions.

Study plots were selected based on uniformity of vegetation structure within and among plots, with a preference for areas of sparse cover by shrubs (mostly western snowberry *Symphoricarpos occidentalis*, and meadow-sweet *Spiraea alba*) or trees (quaking aspen *Populus tremuloides* and willow *Salix* spp).

The median (5th–95th percentile) cover by shrubs and trees within study plots was 0.7% (0–12%), and the median (5th–95th percentile) cover by shrubs and trees within 1 km of study plots was 9.6% (1.5–29.3%). Some study plots were purposefully chosen adjacent to areas with high percent tree cover for evaluating landscape influence on breeding grassland birds (Winter et al. 2001; MW unpubl. data). The number of study plots varied slightly among years, depending on accessibility and burning regime (Table 1). Study plots were established by placing wooden stakes or flags at 50-m intervals along parallel transects that were 100 m apart. Depending on the size of the prairie patch, the size of study plots varied between 1.65 and 20.64 ha (mean = 11.22 ± 0.88 ha), with small prairie patches containing smaller study plots than large patches.

Field methods.—We searched for nests of the three most common grassland birds, Clay-colored and Savannah sparrows and Bobolinks, between 15 May and 31 July each year. Nests were found by flushing birds from nests while walking systematically or haphazardly through the study plots, or by behavioral observations (see Winter et al. 2003). We marked each nest with a pink surveyor flag 5 m north of the nest and revisited nests every 2–4 days to determine outcome. A nest was considered successful if at least one young of the parental species fledged, and it was considered parasitized if it contained at least one egg or young of a Brown-headed Cowbird. The number of young fledged was assumed to be equal to the number of young observed on the last nest check if we did not find any indication of nest loss. We determined nest initiation dates by backdating nests with known hatching or fledging dates, assuming that one egg was laid per day and that incubation started with the last egg laid.

After fledging or failure, we measured nest-site characteristics at five locations: directly at the nest and 0.5 m from the nest in each cardinal direction (Winter 1999). At each location we estimated percent cover of bare ground, grass, forb, litter (dead plant material), and shrub within a 20 × 50 cm Daubenmire frame (Daubenmire 1959). We placed a meter stick about 5 cm from each outer corner of the Daubenmire frame to measure the

height of the highest plant touching the stick (“vegetation height”) and litter depth. “Litter depth” was defined as the depth at which dead plant material lying at an angle of less than 45° completely covered a ruler when viewed from the side. We placed a Robel pole (Robel et al. 1970) in the middle of each Daubenmire frame and took visual obstruction readings to the nearest 0.5 dm at a distance of 4 m from each cardinal direction. We determined the average values for ground cover, vegetation height, litter depth, and visual obstruction for the five locations, and used those average values in all analyses. At each nest, we measured the height (cm) above ground of the bottom of the nest cup and determined the nest substrate (bare ground, grass, forb, litter, or shrub). “Nest substrate” was defined as the substrate on which >50% of the nest was built. We also estimated what percent of a nest was covered by vegetation when viewed from above, and the distance (m) between the nest and the closest shrub and tree.

Data analyses.—Winter et al. (in press) demonstrated that nest success did not vary enough among years and regions to be detected statistically. Therefore, we combined data from all regions and years. However, because nesting parameters will always vary somewhat among regions and years, we took this variation into account by including region and year as random effects in all analyses. We also included year as a repeated effect, because nests were found on the same prairies during several years. We compared nest-site characteristics, nest phenology, and different parameters of breeding performance among species with the Tukey-Kramer test of multiple comparisons in PROC MIXED (SAS Institute, Inc. 1999). We analyzed data on (1) the initiation dates for the first nest; (2) the percentage of nests with bare ground, litter, forb, or shrubs as the main substrate; (3) the percentages of unsuccessful nests, nests with partial depredation, and parasitized nests; and (4) the average values for nest-site characteristics, clutch size, number of eggs hatched, and number of young fledged. In each analysis, each species-year-study plot combination was represented by a single data point. For all analyses except nest initiation and clutch size, we excluded study plots on which we found fewer than five nests of a given species; thus,

sample size (n) equals the number of study plots on which we found >4 nests of a species. The number of nests used to determine clutch size, hatching success, and fledging success differs from the number of nests used to describe nest-site characteristics because we were not able to relocate some nests after they were terminated. In addition, some nests were part of an allied study in which we used miniature video cameras at nest sites to determine the types of nest predators visiting a nest. We did not include nest-fate data from camera-monitored nests because of the potential influence that video cameras had on nest success (Pietz and Granfors 2000), but we did include those nests in our summary of nest-site characteristics.

While we evaluated whether a species' clutch size changed during the breeding season using PROC MIXED (SAS Institute, Inc. 1999), the binomial (success/fail) nature of data on nesting success made other analysis procedures necessary. For these data, we used the GLIMMIX macro (Wolfinger and O'Connell 1993) in conjunction with Shaffer's logistic-exposure model (Shaffer 2004, see below). For the analysis of clutch size, we excluded nests that were discovered after hatching to minimize the possibility that clutch size had been reduced by partial predation. We used Akaike's Information Criterion (AIC; Anderson et al. 2000) to determine which of seven different date models best described seasonal changes in clutch size and nest success. The date models included date in linear, squared, linear plus squared, logarithmic, exponential, linear plus exponential, or categorical form. To compare clutch size, number of eggs hatched, and number of fledglings between parasitized and nonparasitized nests of the same species, we used PROC TTEST (SAS Institute, Inc. 1999). Results are presented as percentages or as means \pm SE.

We calculated two estimates of nest success: (1) Mayfield estimates (Mayfield 1975), and (2) estimates from logistic-exposure models (Shaffer 2004). To calculate the number of exposure days for the Mayfield estimate, we determined the mid-point between the penultimate and the ultimate date of nest checking. The number of exposure days for nests with unknown fate included only the number of days until the penultimate date of nest check-

ing (Manolis et al. 2000). Standard errors for daily nest survival rates follow Johnson (1979). Whereas the Mayfield method requires nests to be grouped into discrete categories, the logistic-exposure method allows each nest to have unique values of covariates. Therefore, this method is more appropriate when investigating factors that might influence nest success. For this analysis, we split the data into two nesting intervals (before and after the penultimate check date), such that the number of observation intervals used in the analysis is greater than the number of nests. To estimate the probability of nest survival over the nesting period (incubation and nestling stages), we took the daily nest survival rates derived from the Mayfield estimates and from the logistic-exposure models to the following exponents: 20 (days) for Clay-colored Sparrow, 21.5 for Savannah Sparrow, and 24 for Bobolink (Ehrlich et al. 1988).

RESULTS

We found 1,795 nests of the three species: 793 Clay-colored Sparrow nests, 687 Savannah Sparrow nests, and 315 Bobolink nests. Nest-site characteristics of Clay-colored Sparrows differed greatly from those of Savannah Sparrows and Bobolinks, whereas nest sites of Savannah Sparrows and Bobolinks were more similar to each other (Table 2). Clay-colored Sparrows placed their nests more frequently in shrubs and less frequently in litter. Consequently, Clay-colored Sparrow nests were higher above ground, the vegetation surrounding the nest had less grass and litter cover and more shrub cover, vegetation was taller, visual obstruction readings were higher, and nests were situated closer to shrubs and trees than those of the other two species. Nest substrates were similar for Savannah Sparrows and Bobolinks. Both species placed their nests most frequently within thick clumps of litter and least frequently in shrubs, but they also differed in several nest-site characteristics (Table 2): Savannah Sparrow nests had a higher percentage of nest cover, and the area surrounding the nests had a slightly higher percentage of bare ground. In addition, vegetation was shorter at Savannah Sparrow nests than at Bobolink nests.

The earliest nest initiation dates were 17 May for Clay-colored Sparrows, 15 May for

TABLE 2. Nest-site characteristics of three passerine species nesting in tallgrass prairie in Minnesota and North Dakota, 1998–2002. Means sharing the same letter (within rows) are not significantly different ($P > 0.05$).

Nest characteristic ^a	Clay-colored Sparrow		Savannah Sparrow		Bobolink	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Nest substrate (%) ^b						
Bare ground	0.2 A	1.5	5.9 B	1.7	3.4 AB	2.1
Grass	8.9 A	2.2	9.5 A	2.7	13.9 A	3.2
Forb	10.4 A	1.8	1.1 B	2.1	6.0 AB	2.6
Litter	33.2 A	3.3	79.5 B	3.9	74.2 B	4.8
Shrub	42.9 A	2.4	0.3 B	2.9	0.7 B	3.5
Nest cover (%)	71.0 AB	1.8	77.2 A	2.0	67.1 B	2.5
Nest height (cm)	13.5 A	0.4	0.2 B	0.5	0.1 B	0.6
Ground cover (%)						
Bare ground	0.9 AB	0.3	1.7 B	0.3	0.3 A	0.4
Grass	27.3 A	1.2	35.1 B	1.4	35.3 B	1.7
Forb	21.1 A	1.3	20.2 A	1.5	22.6 A	1.9
Litter	29.2 A	1.3	41.5 B	1.5	38.6 B	1.9
Shrub	21.4 A	0.1	1.3 B	1.2	2.6 B	1.5
Litter depth (cm)	4.9 A	0.3	4.0 B	0.3	4.8 AB	0.4
Vegetation height (cm)	48.7 A	1.0	33.2 B	1.1	39.1 C	1.4
Visual obstruction (dm)	3.8 A	0.1	1.7 B	0.1	2.1 B	0.2
Distance (m) of nest to						
Shrubs	11.0 A	3.3	32.7 B	3.7	36.8 B	4.7
Trees	99.2 A	21.5	219.8 B	24.3	192.9 B	30.6

^a We used average nest characteristics for each species, region, year, and study plot, excluding prairies in which <5 nests were found; $n = 137$ plot-years for the analysis on nest substrate; $n = 134$ for all other analyses.

^b Nest substrate was defined as that on which >50% of the nest was built.

Savannah Sparrows, and 29 May for Bobolinks (Fig. 1). Dates of nest initiation did not differ between Savannah Sparrows and Clay-colored Sparrows ($P = 1.00$), whereas nest initiation for Bobolinks was about 2 weeks later than that of the other two species (both comparisons: $P < 0.001$, $n = 248$). Clay-colored Sparrows initiated most nests between mid-May and the end of June. For Savannah Sparrows, nest initiations were most frequent between late May and mid-June, but peaks in nest initiation were inconsistent among years and regions. Bobolinks initiated most of their nests from early to mid-June; almost no nests were initiated in July. The single nesting peak during a relatively short breeding season provides evidence for single-brooding of Bobolinks in our study region.

For each species, clutch size generally decreased during the breeding season (Fig. 2). The best model describing changes in clutch size included both linear and squared values of date. For Clay-colored Sparrows, the best model (Akaike weight = 0.83, $n = 582$) was

more than nine times as well supported as the next best model that included the squared date alone (Akaike weight = 0.09), whereas the best model for Savannah Sparrows (Akaike weight = 0.62) was less than three times as well supported as the null model (Akaike weight = 0.23, $n = 387$). For Bobolinks, the best model (Akaike weight = 0.29, $n = 184$) did not clearly differ from models that included date as squared, linear, logarithmic, or linear plus exponential value (each model had an Akaike weight >0.08).

Probability of daily nest survival decreased with time during the breeding season in Clay-colored Sparrows and Bobolinks (Fig. 3). The best model for both Clay-colored Sparrows (Akaike weight = 0.33, $n = 776$) and Bobolinks (Akaike weight = 0.40, $n = 312$) included the logarithmic transformation of date. Even though these models were better than the null model (which had an Akaike weight of zero), daily nest survival was not precisely estimated because of the large standard errors (Fig. 3). Linear and quadratic forms of date

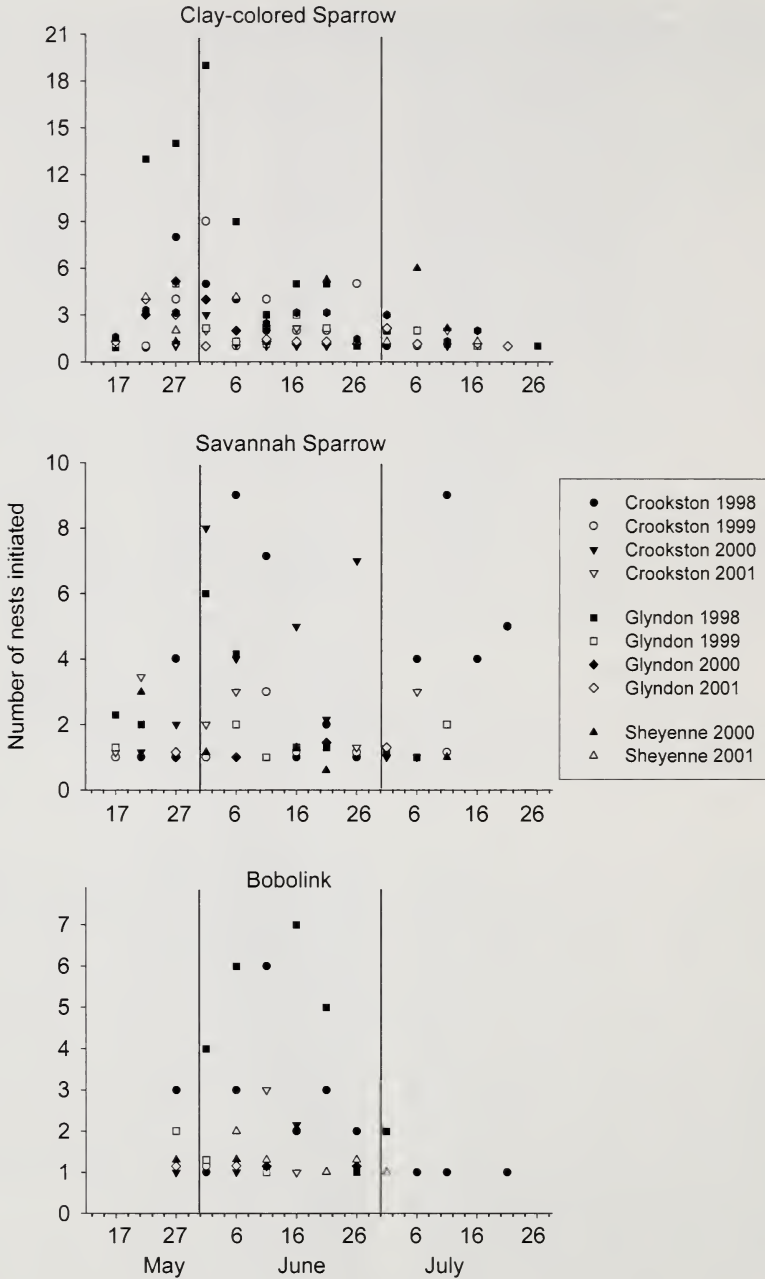


FIG. 1. Number of nests initiated within 5-day periods for three passerine species nesting in northern tallgrass prairie in Minnesota (Crookston and Glyndon regions) and North Dakota (Sheyenne National Grassland), 1998–2002. Dates of nest initiation were calculated by backdating from nests with known hatching or fledging dates; vertical lines distinguish the month in which nests were initiated.

were also well supported in both species (Akaike weight > 0.25). Daily nest survival of Savannah Sparrows did not change with time in the breeding season (Fig. 3); the null

model was better supported (Akaike weight = 0.82, $n = 665$) than any model that included date.

The most important cause of nest failure

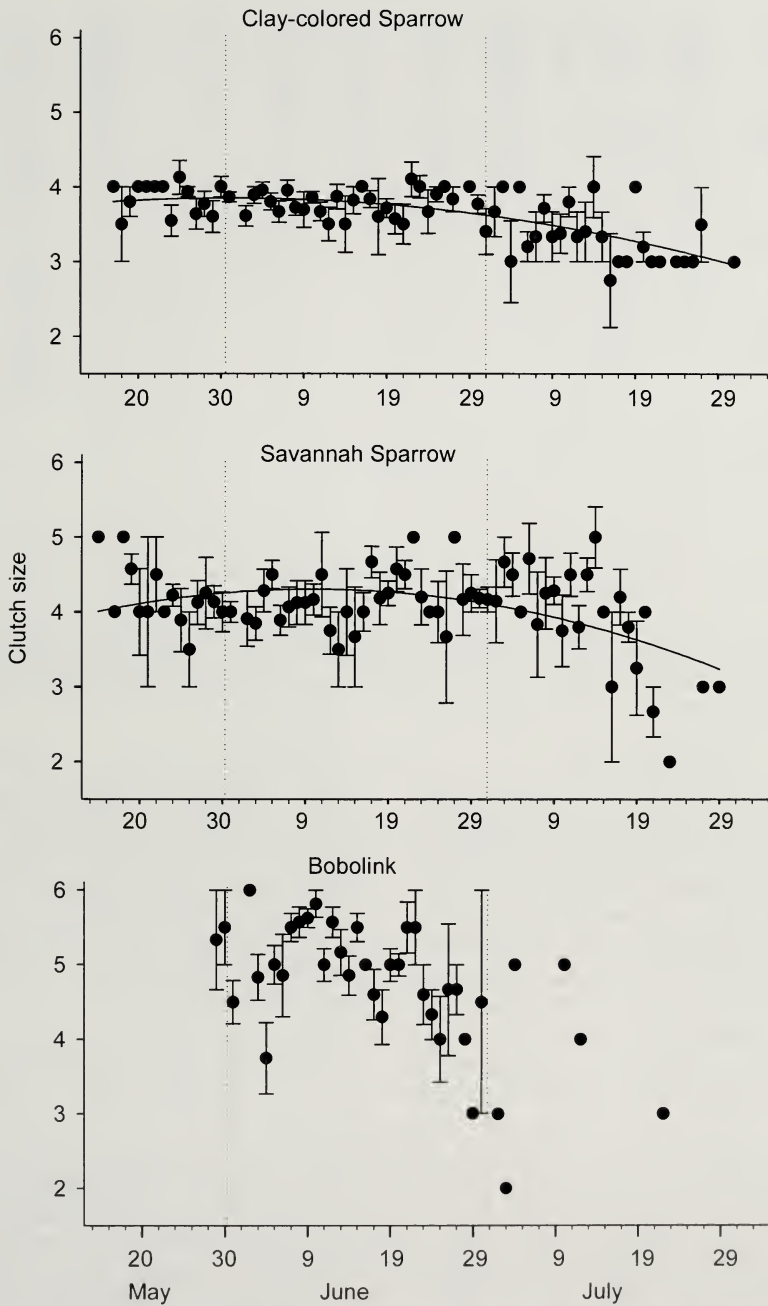


FIG. 2. Changes in clutch size during the breeding season for three species of grassland birds nesting in northern tallgrass prairie in Minnesota and North Dakota, 1998–2002. Each filled circle represents the mean clutch size (\pm SE) by date. Curves indicate predicted values for the best-fitting model that included date as a linear and squared term in a mixed model analysis. For Bobolinks, no line is shown because no single model best fit the data.

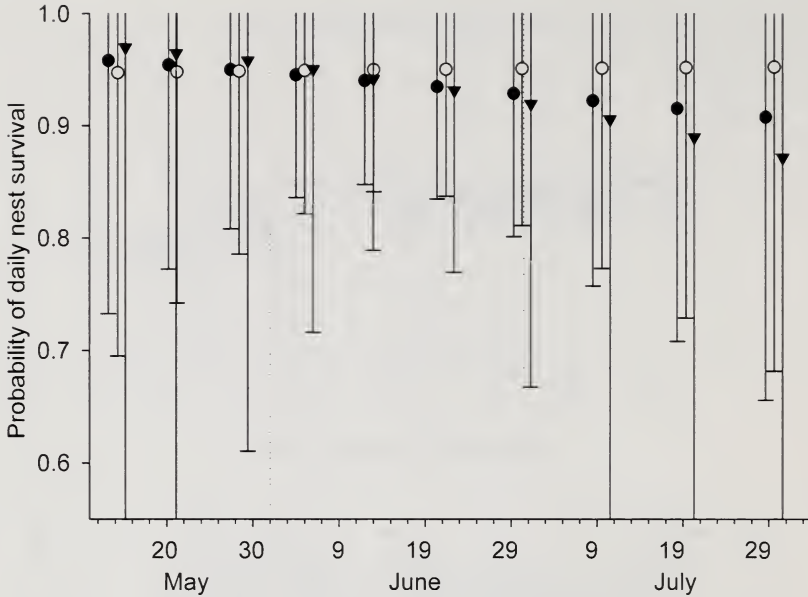


FIG. 3. Estimated daily nest survival (derived from the logistic-exposure method, Shaffer 2004) \pm SE for Clay-colored Sparrows (filled circles, $n = 776$ nests), Savannah Sparrows (open circles, $n = 665$), and Bobolinks (triangles, $n = 312$) at different times during the breeding season in northern tallgrass prairie in Minnesota and North Dakota, 1998–2002.

was nest predation, followed by nest abandonment (Table 3). Nest predation was higher for Clay-colored Sparrows than for Savannah Sparrows, and was intermediate in Bobolinks. In only a few cases did hosts rear only cowbirds (Table 3). The percentage of abandoned nests was similar among species (each comparison: $P > 0.05$), and its main cause—except for unknown factors—was partial nest predation (Table 3). However, we cannot be certain whether partial nest predation occurred before or after the nest was abandoned. Other causes of nest failure were of minor importance. Daily nest survival was highest for Savannah Sparrows, regardless of the estimation method (Table 4). Mayfield daily survival rates were slightly lower than those calculated with the logistic-exposure method (Table 4).

Clutch size was lowest for Clay-colored Sparrows and highest for Bobolinks (Fig. 2, Table 5). Even though the number of eggs hatched per nest was similar between Clay-colored and Savannah sparrows, the number of host young fledged per nest was higher for Savannah Sparrows (Table 5), probably because nest predation was higher in Clay-colored Sparrows (Table 3). Compared with Sa-

vannah Sparrows, Bobolinks had a larger clutch size and more eggs that hatched. In spite of this difference, the number of young fledged per nest was similar between Bobolinks and Savannah Sparrows, possibly because complete and partial nest predation were higher for Bobolinks than for Savannah Sparrows (Table 3).

Brood parasitism was lower for Clay-colored Sparrows than for Bobolinks ($P = 0.017$, $n = 135$), whereas it did not differ between Savannah Sparrows and either Clay-colored Sparrows or Bobolinks (each comparison: $P > 0.24$; Table 3). The number of cowbird eggs per parasitized nest was lower for Clay-colored Sparrows than for Savannah Sparrows ($P = 0.028$, $n = 34$) but did not differ from that for Bobolinks ($P = 0.64$; Table 5). Parasitized nests had smaller host clutch sizes than nonparasitized nests for Clay-colored Sparrows ($t = 2.92$, $P = 0.016$, $n = 335$), Savannah Sparrows ($t = 2.30$, $P = 0.034$, $n = 238$), and Bobolinks ($t = 1.79$, $P = 0.077$, $n = 103$; Table 5). For each species, the number of host eggs hatched in nonparasitized nests was higher than in parasitized nests (Clay-colored Sparrows: $t = 3.55$, $P < 0.001$, $n = 393$; Sa-

TABLE 3. Causes of egg and nestling mortality for three passerine species nesting in northern tallgrass prairie in Minnesota and North Dakota, 1998–2002. Means sharing the same letter (within rows) are not significantly different ($P > 0.05$).

	Clay-colored Sparrow ($n = 781$) ^a	Savannah Sparrow ($n = 675$) ^a	Bobolink ($n = 314$) ^a
Complete nest loss due to			
Predation (%)	47.9 A	33.5 B	41.8 AB
Weather (%)	1.4 A	1.5 A	1.9 A
Trampling (%)	1.3 A	0.6 A	2.5 A
Cowbird parasitism (%) ^b	0.8 A	1.5 A	1.6 A
Burning (%)	0.4 A	0.0 A	0.0 A
Abandonment (%) ^c	8.8 A	6.4 A	8.0 A
Partial predation (%)	30.8	25.6	36.0
Cowbird parasitism (%)	16.2	18.6	12.0
Banding (%) ^d	14.7	20.9	12.0
Weather (%)	2.9	11.6	16.0
Unknown cause (%)	35.4	23.3	24.0
Unknown fate (%)	0.4	0.6	1.0
Partial predation at any nesting stage (%)	9.3 A	9.5 A	13.7 B
Cowbird parasitism (%) ^c	5.1 A	6.7 AB	10.8 B

^a Number of nests used in the analysis.

^b Nests were completely lost to cowbirds if cowbirds removed all eggs or young from the nest.

^c Includes only those nests that were known to be abandoned or not (CCSP: $n = 776$, SAVS: $n = 668$, BOBO: $n = 311$).

^d As part of a study on annual return rates (T. M. Donovan unpubl. data), some birds were banded in the Crookston region.

^e Percentage of nests parasitized by Brown-headed Cowbirds.

vannah Sparrows: $t = 2.95$, $P < 0.001$, $n = 302$; Bobolinks: $t = 1.89$, $P = 0.061$, $n = 123$; Table 5). Consequently, more host young fledged from nonparasitized than from parasitized nests (Clay-colored Sparrow: $t = 5.77$, $P < 0.001$, $n = 778$; Savannah Sparrow: $t = 13.46$, $P < 0.001$, $n = 669$; Bobolink: $t = 5.15$, $P < 0.001$, $n = 313$; Table 5). Similar differences in the number of host young fledged were also found for nonparasitized and parasitized successful nests (in each comparison: $t > 3.2$, $P < 0.01$; Table 5).

DISCUSSION

The differences in breeding parameters among species that we studied suggest that one common management practice, the use of "indicator species," cannot be used indiscriminately in the conservation of grassland bird communities. Different management actions will benefit different sets of species. For example, early haying might not be detrimental to the relatively late-arriving Bobolink, but would destroy nests of Clay-colored and Savannah sparrows, whereas removal of shrubs

TABLE 4. Estimates of daily nest survival and nest success for three passerine species nesting in northern tallgrass prairie in Minnesota and North Dakota, 1998–2002.

	Clay-colored Sparrow	Savannah Sparrow	Bobolink
Number of nests	793	687	315
Number of unsuccessful nests	460	286	163
Exposure days	7333.5	5456	2564
Days of nesting (interval length) ^a	20	21.5	24
Mayfield daily nest survival rate \pm SE ^b	0.937 \pm 0.003	0.948 \pm 0.003	0.936 \pm 0.005
Mayfield nest success ^c	0.274	0.314	0.207
Logistic-exposure daily nest survival rate \pm SE ^d	0.940 \pm 0.092	0.950 \pm 0.107	0.939 \pm 0.144
Logistic-exposure nest success ^c	0.288	0.330	0.219

^a Incubation and nestling days (Ehrlich et al. 1988).

^b Mayfield daily nest survival rate (DSR) = $1 - (\text{number of unsuccessful nests}/\text{exposure days})$. SE = $\sqrt{(\text{DSR} \times (1 - \text{DSR}))/\text{exposure days}}$.

^c Probability of nesting success over the incubation and nestling intervals = $\text{DSR}^{\text{interval length}}$.

^d Probability of daily nest survival as calculated by the logistic-exposure model (Shaffer 2004).

TABLE 5. Clutch size, hatching success, and fledging success (\pm SE) of parasitized and nonparasitized nests of three passerine species nesting in northern tallgrass prairie in Minnesota and North Dakota, 1998–2002. Means sharing the same letter (within rows) are not significantly different ($P > 0.05$).

	Clay-colored Sparrow			Savannah Sparrow			Bobolink		
	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>
Host clutch size ^a	3.77 A	0.03	335	4.13 B	0.05	238	5.25 C	0.08	103
Nonparasitized nests	3.80 A	0.03	325	4.19 B	0.05	220	5.29 C	0.08	97
Parasitized nests	3.10 A	0.23	10	3.50 AB	0.29	18	4.67 B	0.49	6
Number of cowbird eggs	1.00 A	0.00	10	1.50 B	0.12	18	1.33 AB	0.21	6
Host eggs hatched/nest ^b	2.52 A	0.09	393	2.41 A	0.11	302	3.46 B	0.20	123
Nonparasitized nests	2.59 A	0.09	372	2.49 A	0.12	280	3.57 B	0.21	114
Parasitized nests	1.24 A	0.29	21	1.32 A	0.27	22	2.11 A	0.75	9
Host young fledged/nest	1.35 A	0.06	778	2.01 B	0.07	669	1.97 B	0.13	313
Nonparasitized nests	1.40 A	0.06	738	2.13 B	0.08	624	2.12 B	0.14	279
Parasitized nests	0.45 A	0.15	40	0.33 A	0.11	45	0.71 A	0.24	34
Host young fledged/successful nest	3.28 A	0.05	320	3.50 A	0.05	385	4.11 B	0.12	150
Nonparasitized nests	3.32 A	0.05	311	3.55 B	0.05	375	4.21 C	0.12	141
Parasitized nests	2.00 A	0.33	9	1.50 A	0.27	10	2.67 A	0.47	9

^a Clutch size was determined only for nests that were monitored during incubation.

^b Hatching success was determined only for nests that were monitored during both the incubation and nestling stages.

would benefit Bobolinks and Savannah Sparrows but limit Clay-colored Sparrows. If any of these species were used as indicator species for developing management guidelines, other species would be mismanaged. Grassland management therefore needs to incorporate the most important aspects of the breeding ecology of each species of interest. Baseline and species-specific data—as provided in our study—are needed to understand which aspects are most important to consider for management actions in a certain area.

Not surprisingly, nest-site characteristics of Savannah Sparrows and Bobolinks were more similar to each other than to those of Clay-colored Sparrows. Clay-colored Sparrows are more a shrubland species than a pure grassland species (Knapton 1994). Savannah Sparrows and Bobolinks, on the other hand, prefer nesting within dense clumps of litter and grass (Dechant et al. 2003b, Dieni and Jones 2003, Swanson 2003). Despite the similar nest-site requirements of Savannah Sparrows and Bobolinks, several nest-site characteristics differed (Table 2), indicating that management practices will differentially affect even those species that have seemingly similar habitat requirements.

The timing of nesting differed markedly between the two grassland sparrows and Bobolinks, with Bobolinks nesting about 2 weeks later than Clay-colored and Savannah spar-

rows. Double-brooding has been reported previously for Clay-colored Sparrows (Knapton 1978) and Savannah Sparrows (Lein 1968, Wiens 1969, Wheelwright and Rising 1993), and the long breeding season (Fig. 1) at our study area makes it likely that Clay-colored and Savannah sparrows raised two broods there as well. For Bobolinks, the breeding season is probably too short for raising two broods (see Gavin 1984). Even though Clay-colored Sparrows fledged less than two young per nest at our study sites (Table 5), double-brooding might result in high-enough seasonal fecundity to ensure population survival. Clutch sizes were similar to those reported elsewhere (Wheelwright and Rising 1993, Martin and Gavin 1995, Swanson 1996, Davis 2003). In each species, clutch size generally decreased during the breeding season, as is well known for many passerines (Dhondt et al. 2002).

Daily nest survival decreased during the breeding season in Clay-colored Sparrows and Bobolinks, but did not change noticeably in Savannah Sparrows. The model including log (date) was the best of those we tested, but there was considerable variation in our estimates (Fig. 3). Differences among species in timing of breeding and in changes of clutch size and daily nest survival over the season indicate that there is no certain time period in which the entire grassland bird community is

least susceptible to disturbances. Certainly, the best timing for any management is before the main nesting season starts (mid-May) or after the main nesting season is over (early August) to minimize disturbances to clutches, young, and fledglings.

In our study, the percentage of successful Clay-colored Sparrow nests was generally higher (28.8%) than that reported in most other areas studied: 13.9% of nests were successful in Saskatchewan ($n = 84$; Davis 2003), and 25.5% ($n = 49$) and 52.2% ($n = 24$) of all nests were successful in Waterfowl Production Areas in North Dakota and Minnesota, respectively (Koford 1999, data recalculated for incubation and nestling period only). Nest success of Savannah Sparrows in our study (33.0%) was higher than that reported for Saskatchewan (22.7%, $n = 84$; Davis 2003) and Manitoba (7%, $n = 30$; Davis and Sealy 2000), and was similar to that reported in Waterfowl Production Areas in Minnesota (33.2%, $n = 30$; Koford 1999). For Bobolinks, nest success was lower in Minnesota (14.2% and 15.8% in two types of planted cover, total $n = 47$; Koford 1999) than in our study (21.9%). Higher Bobolink nest success was reported for New York (54.5%, $n = 422$; Martin and Gavin 1995) and Wisconsin (52.4%, $n = 103$; Martin 1971), but those values are apparent rates of nest success, which are biased high, possibly by a factor of two (Johnson 1979). Most of the nest failures documented in our study were due to predation, similar to what was found by Martin (1993) and Davis (2003).

Brood parasitism is assumed to be higher close to shrubs and trees because woody vegetation may harbor more Brown-headed Cowbirds (Johnson and Temple 1990, Romig and Crawford 1995, Saunders et al. 2003). Because nests of Clay-colored Sparrows were closer to woody vegetation and were higher off the ground than nests of Savannah Sparrows and Bobolinks (Table 2), we expected Clay-colored Sparrows to have higher rates of brood parasitism than the other two species (Fleischer 1986, Davis and Sealy 2000). However, brood parasitism by cowbirds was lower in Clay-colored Sparrows (5.1%) than in Bobolinks (10.8%), whereas in Savannah Sparrows it was intermediate (6.7%). Larger birds might be more conspicuous than more-secre-

tive grassland sparrows, facilitating detection by female cowbirds (Davis and Sealy 2000, Koford et al. 2000). However, Bobolink—the largest grassland bird in our study—is also an icterid, and a preference of cowbirds for icterine species might have a phylogenetic basis (Hanka 1979).

Clay-colored Sparrows had lower parasitism (5.1%) than that reported for any other area (range: 10–39%; Shaffer et al. 2003). Similarly, brood parasitism in Savannah Sparrows was lower (6.7%) than that reported in most other studies (range: 2–37%; Shaffer et al. 2003). Brood parasitism of Bobolinks (10.8%) was intermediate to that recorded in other studies (range: 0–34%; Shaffer et al. 2003). Even though parasitized nests fledged one to two fewer young than nonparasitized nests, cowbirds probably do not have a significant effect on grassland bird populations in our study area because the intensity of parasitism there is low.

Several factors might be responsible for low levels of nest predation and cowbird parasitism found in our study area (MW unpubl. data). Some of the most likely factors were (1) study plots were located in relatively large patches of continuous grassland [median = 61.3 ha, 8.0–1,245.6 ha (5th–95th percentile)], and nest predation and cowbird parasitism is frequently lower in large grassland patches (Winter and Faaborg 1999, Herkert et al. 2003); (2) study plots were located in a landscape with relatively little shrub and tree cover within 1 km [median = 9.6%, 1.5–29.3% (5th–95th percentile)], and nest predation and cowbird parasitism is frequently lower far from woody vegetation (Johnson and Temple 1990, Davis and Sealy 2000, Winter et al. 2000); and (3) few cattle were present in the study area (except for Sheyenne National Grassland), and cowbird parasitism is frequently lower far from grazed areas (Davis and Sealy 2000, Goguen and Matthews 2000). Proximity of our study area to the center of the cowbird's range (Lowther 1993) may not result in high brood parasitism, because cowbird parasitism can be largely independent of cowbird density (Goguen and Matthews 2000).

In summary, grassland birds in our study area appear to be more successful than in most other areas where their nesting parameters

have been investigated; nest success was higher, and cowbird parasitism was lower than in most other studies. Northwestern Minnesota and southeastern North Dakota provide some of the largest remaining tracts of native tall-grass prairie, many of which are surrounded by large tracts of reseeded grasslands and little forest cover (MW unpubl. data). These features probably contribute to quality habitats for nesting grassland birds.

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CLIMATE CHANGE AS REFLECTED IN A NATURALIST'S DIARY, MIDDLEBOROUGH, MASSACHUSETTS

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ABSTRACT.—Observations by local naturalists may provide valuable records of phenological events with which we can measure the response of species to climate change. To test this idea, we examined the records of a dedicated naturalist who has been observing bird arrivals, plant flowering, butterfly appearance, and frog calling on her farm in Middleborough, southeastern Massachusetts. From her 1970 to 2002 records, we extracted data on first observations of spring phenological events for 24 species—650 observations in all. Over that time, average annual local temperatures rose by 2.0° C. Twenty-two species showed earlier activity, with 5 of the 16 bird species now arriving significantly earlier in the year than they did 30 years ago. Twenty-two species responded to warming temperatures, with 4 species (two birds, one frog, and one plant) showing statistically significant earlier activity in years with warmer temperatures. The other 18 species showed similar trends, but they were not statistically significant. *Received 17 February 2004, accepted 12 August 2004.*

Many species have demonstrated phenological responses to climate change (Walther et al. 2002, Parmesan and Yohe 2003, Root et al. 2003). These responses were reflected in earlier timing for events such as bird migrations (Oglesby and Smith 1995, Ahas 1999), plant flowerings (Sparks and Carey 1995, Bradley et al. 1999), insect appearance (Sparks and Yates 1997), and amphibian breeding (Beebee 1995, Gibbs and Breisch 2001). In order to characterize the variation of these effects across species, landscapes, and regions, scientists have used long-term records of phenological observations from selected localities. Thus far, most studies have relied upon records from historical data sets collected systematically, often as part of formal research projects (Whitfield 2001), or collected in a rigorous manner by scientists at field stations (Fitter et al. 1995, Sparks and Carey 1995, Bradley et al. 1999, Inouye et al. 2000). For example, a recent study, which used formal data collection efforts of ornithological societies in New York and Massachusetts, has shown that many migrant bird species in eastern North America have been arriving earlier over the last 100 years (Butler 2003). Unfortunately, formal (often professionally collected), long-term phenological data sets such as these are rare and difficult to find for many regions and species.

We believe that observations made by local naturalists can fill in the gaps and expand our knowledge of the effects of global warming. Naturalists in fields such as birding, field botany, gardening, fishing, and hunting often keep daily journal records of phenological events. Many of their records include information on the specific date and location of the observations. Perhaps the most common records are those of people who simply record what they see around their homes or on daily walks, such as the first flowering of plants or first migrant bird in the spring. We suspect that large numbers of such naturalists' records exist and are widely distributed across the globe. However, the value of these collections of observations in demonstrating species' responses to climate change remains in question. Will irregularities in the data collection, such as long periods without observations or inconsistent sampling effort, mask any real trends present in nature? Or are the biological changes robust enough to appear even in imperfect data sets? If naturalists' records do reflect phenological responses to climate change, they could open up a greatly expanded range of data for climate change research, covering places and species for which there are no formal research studies.

We already have strong evidence in eastern Massachusetts that birds are arriving and plants are flowering earlier in response to warming temperatures (Butler 2003, Primack et al. 2004). Thus, the primary purpose of this project was to test whether the journal entries

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of a local naturalist could detect long-term changes in phenological events and the responses of numerous species to changes in springtime temperatures. To accomplish this, we examined the observations of a naturalist, who from 1970 to 2002 recorded the dates of many phenological events on her farm in Middleborough, Massachusetts.

METHODS

Kathleen S. Anderson is an active naturalist who has been involved for many decades in conservation issues at local, regional, and national levels. For example, from 1969 to 1983, she served as the director of the Manomet Bird Observatory (now Manomet Center for Conservation Sciences), one of the most active centers for ornithological banding and research in New England. For the last 53 years, she has lived on a 40-ha farm in Middleborough, 49 km south of Boston and 23 km from the Atlantic Ocean. Her farm consists mainly of second-growth deciduous forest, swampland, and a small pond. She also maintains several farm buildings and a pasture for sheep grazing. Due to a strong personal interest, she has gradually learned more about the natural history of species that occur on her farm. Nearly every day that she was on her farm from 1960 to 2002, Mrs. Anderson recorded the birds, flowering plants, butterflies, and amphibian choruses she saw or heard. Her observations were not systematic, however. For example, some days she made observations while on walks through her farm, while on other days she recorded only what she saw from her back porch. She was also occasionally away from her farm for several days at a time.

Following an examination of Mrs. Anderson's records, we selected a time period (1970 to 2002) during which she had made observations each day she was on the farm. She did not begin recording observations with enough regularity for statistical analysis until 1970. We selected common species that she had observed on her farm during at least half of the years from 1970 to 2002. We examined her journals for the arrival dates of 16 migratory bird species, the first flowering of 3 plant species, the first appearance of 2 butterfly species, and the first spring chorus of 3 amphibian species (Table 1). By 1970, Mrs. Anderson had

lived on her farm for 20 years and had made observations of spring phenological events for 10 years. She was thoroughly familiar with, and able to identify, each of the species that we selected. Thus, we are confident that there was no bias caused by increasing familiarity with the species over time.

From each of her narrative-style journals, we extracted the date of first observation for each of the events mentioned above. We did not correct for any gaps in the data that were caused by her being away from the farm or not recording any observations. We then used regression analysis to examine the relationships between the timing of each phenological event and the year. We also used regression analysis to examine the relationships between the timing of phenological events and temperatures in late winter and spring. Our temperature data were taken from Rochester, Massachusetts, 11 km from Middleborough [National Oceanic and Atmospheric Administration (NOAA), Northeast Regional Climate Center, Ithaca, New York]. For all bird species, regression analyses were based on the mean temperature of the month of arrival and that of the previous month, as provided by NOAA; thus, for a bird that arrived in April, we regressed its arrival date on the mean March–April temperature (see Table 2). For the plant, amphibian, and butterfly species, we regressed the date of first spring activity on the mean temperature of the time period from 1 February through the month when first activity was observed. Statistical significance was set at $P = 0.05$; we used Microsoft Excel 98 for all regression analyses.

RESULTS

Trends over time.—Over the last 33 years, mean annual temperatures in Rochester, Massachusetts have risen an average of 0.7°C per decade, for a total increase of 2.0°C (NOAA, Northeast Regional Climate Center, Ithaca, New York; Fig. 1). Given the warming trend, we hypothesized that Mrs. Anderson's records could demonstrate that species are responding to warmer climate by exhibiting earlier spring phenologies.

Of the 16 bird species, 5 species—Wood Duck (*Aix sponsa*), Ruby-throated Hummingbird (*Archilochus colubris*), House Wren (*Troglodytes aedon*), Ovenbird (*Seiurus au-*

TABLE 1. Results of regressions of first spring activity on year. Slope of the regression line indicates change (in days/year) in first phenological activity. Significant regressions are bold-faced. Observations of first spring activity were made by K. S. Anderson in Middleborough, Massachusetts, 1970–2002.

Species	Slope	R ²	P	n ^a
Birds				
Wood Duck (<i>Aix sponsa</i>)	-1.01	0.43	<0.001	30
Ruby-throated Hummingbird (<i>Archilochus colubris</i>)	-0.58	0.18	0.023	28
Tree Swallow (<i>Tachycineta bicolor</i>)	-0.27	0.05	0.21	31
Barn Swallow (<i>Hirundo rustica</i>)	-0.06	0.00	0.84	24
House Wren (<i>Troglodytes aedon</i>)	-0.26	0.14	0.046	28
Hermit Thrush (<i>Catharus guttatus</i>)	-0.44	0.05	0.24	27
Wood Thrush (<i>Hylocichla mustelina</i>)	-0.12	0.07	0.21	23
Gray Catbird (<i>Dumetella carolinensis</i>)	-0.09	0.05	0.24	30
Yellow Warbler (<i>Dendroica petechia</i>)	-0.52	0.12	0.075	27
Pine Warbler (<i>Dendroica pinus</i>)	-0.52	0.04	0.33	23
Black-and-white Warbler (<i>Mniotilta varia</i>)	0.08	0.03	0.30	33
Ovenbird (<i>Seiurus aurocapillus</i>)	-0.15	0.16	0.025	32
Chipping Sparrow (<i>Spizella passerina</i>)	-0.78	0.18	0.019	30
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	-0.21	0.06	0.18	30
Common Grackle (<i>Quiscalus quiscula</i>)	0.34	0.06	0.21	30
Baltimore Oriole (<i>Icterus galbula</i>)	-0.12	0.07	0.22	24
Plants				
Goldthread (<i>Coptis trifolia</i>)	-0.19	0.06	0.21	28
Spicebush (<i>Lindera benzoin</i>)	-0.08	0.02	0.55	21
Wood-anemone (<i>Anemone quinquefolia</i>)	-0.07	0.01	0.59	28
Amphibians				
American toad (<i>Bufo americanus</i>)	-0.29	0.05	0.29	22
Spring peeper (<i>Pseudacris crucifer</i>)	-0.54	0.06	0.17	31
Wood frog (<i>Rana sylvatica</i>)	-0.12	0.01	0.64	30
Insects				
Mourning cloak (<i>Nymphalis antiopa</i>)	-0.04	0.00	0.94	19
Spring azure (<i>Celastrina ladon</i>)	-0.14	0.02	0.53	24

^a Number of years for which there were observations.

rocapilla), and Chipping Sparrow (*Spizella passerina*)—showed statistically significant trends toward earlier spring arrival times (all $P < 0.05$). The strongest trend was for Wood Ducks, which, on average, arrive 32.2 days earlier than they did 32 years ago, as determined by straight-line regression analysis (Table 1, Fig. 2A). Ruby-throated Hummingbirds now arrive, on average, 18.4 days earlier than they did 32 years ago. Of the other 11 species, 9 showed non-significant trends (all $P > 0.05$) toward earlier arrivals (negative slopes) and two species—Black-and-white Warbler (*Mniotilta varia*) and Common Grackle (*Quiscalus quiscula*)—showed non-significant trends toward later arrivals (positive slopes). While none of the plant, butterfly, or amphibian species had statistically significant earlier phenologies over time, they all showed progres-

sively earlier spring activity over time, as shown by negative slopes of arrival time in successive years. Overall, 22 of the 24 species showed trends toward earlier spring activity, more than would be expected by chance ($\chi^2 = 16.7$, $df = 1$, $P < 0.001$). The average rate of response for all observed spring phenological events (all 24 species) was 2.6 days earlier per decade, or 8.3 days for the overall time period.

Trends as temperatures increase.—First occurrence in 4 of the 24 species—Wood Duck, Red-winged Blackbird (*Agelaius phoeniceus*), goldthread (*Coptis trifolia*), and spring peeper (*Pseudacris crucifer*)—showed significant correlations (all $P < 0.05$) with spring temperatures (Table 2, Fig. 2B). In each case, species showed a statistically significant tendency to exhibit earlier spring phenologies in years

TABLE 2. Results of regressions of first spring activity on mean monthly temperatures. Slope of the regression line indicates change (in days/°C) in first phenological activity. Significant regressions are bold-faced. The number of years of observation is given in Table 1. Observations of first spring activity were made by K. S. Anderson in Middleborough, Massachusetts, 1970–2002.

Species	Slope	R ²	P	Correlation timeframe
Birds				
Wood Duck (<i>Aix sponsa</i>)	-6.21	0.43	0.001	Feb–Mar
Ruby-throated Hummingbird (<i>Archilochus colubris</i>)	0.55	0.02	0.53	Apr–May
Tree Swallow (<i>Tachycineta bicolor</i>)	-1.04	0.07	0.16	Mar–Apr
Barn Swallow (<i>Hirundo rustica</i>)	0.81	0.04	0.33	Apr–May
House Wren (<i>Troglodytes aedon</i>)	-0.57	0.06	0.21	Apr–May
Hermit Thrush (<i>Catharus guttatus</i>)	-0.87	0.02	0.51	Mar–Apr
Wood Thrush (<i>Hylocichla mustelina</i>)	-0.14	0.01	0.66	Apr–May
Gray Catbird (<i>Dumetella carolinensis</i>)	-0.31	0.05	0.25	Apr–May
Yellow Warbler (<i>Dendroica petechia</i>)	-0.08	0.00	0.94	Apr–May
Pine Warbler (<i>Dendroica pinus</i>)	-0.65	0.01	0.63	Mar–Apr
Black-and-white Warbler (<i>Mniotilta varia</i>)	-0.20	0.02	0.48	Apr–May
Ovenbird (<i>Seiurus aurocapillus</i>)	-0.31	0.05	0.23	Apr–May
Chipping Sparrow (<i>Spizella passerina</i>)	-0.54	0.01	0.63	Mar–Apr
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	-2.54	0.24	0.006	Feb–Mar
Common Grackle (<i>Quiscalus quiscula</i>)	-2.75	0.10	0.085	Feb–Mar
Baltimore Oriole (<i>Icterus galbula</i>)	-0.81	0.03	0.44	Apr–May
Plants				
Goldthread (<i>Coptis trifolia</i>)	-2.99	0.27	0.004	Feb–Apr
Spicebush (<i>Lindera benzoin</i>)	-0.45	0.04	0.40	Feb–Apr
Wood-anemone (<i>Anemone quinquefolia</i>)	-1.13	0.09	0.12	Feb–May
Amphibians				
American toad (<i>Bufo americanus</i>)	-0.44	0.01	0.66	Feb–Apr
Spring peeper (<i>Pseudacris crucifer</i>)	-3.75	0.17	0.023	Feb–Mar
Wood frog (<i>Rana sylvatica</i>)	-2.86	0.11	0.069	Feb–Mar
Insects				
Mourning cloak (<i>Nymphalis antiopa</i>)	-0.13	0.00	0.93	Feb–Apr
Spring azure (<i>Celastrina ladon</i>)	-1.40	0.11	0.11	Feb–Apr

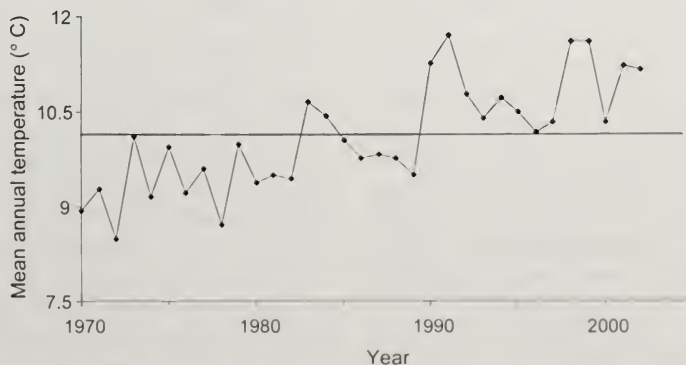


FIG. 1. Mean annual temperatures from 1970 to 2002 at Rochester, Massachusetts (11 km from Middleborough) as reported by NOAA. The horizontal line represents the long-term mean for 1970–2002 (10.1°C).

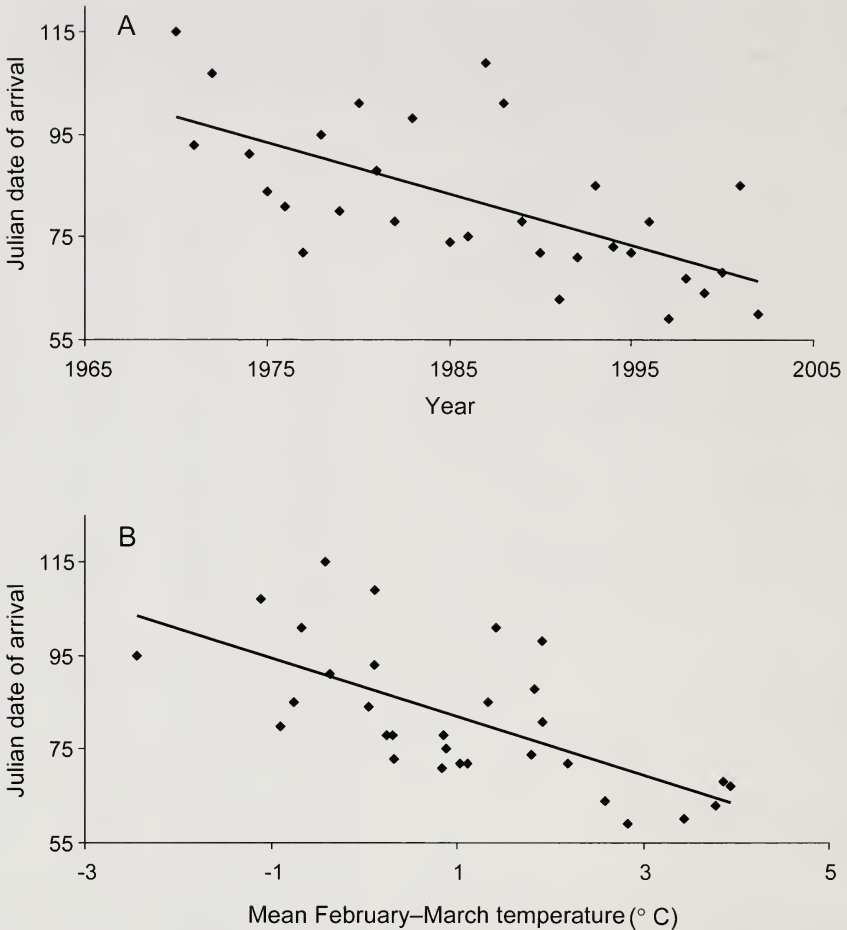


FIG. 2. Wood Duck (*Aix sponsa*) arrival dates (Julian) in Middleborough, Massachusetts for the period 1970–2002: (A) by year and (B) in relation to mean springtime (February–March) temperatures. Lines represent best fit using regression analysis (see Tables 1, 2).

with warmer temperatures. For example, with each 1.0°C increase in mean temperature of the 2 months prior to arrival, Red-winged Blackbirds arrived 2.5 days earlier, Wood Ducks arrived 6.2 days earlier, goldthreads flowered 2.9 days earlier, and spring peepers called 3.7 days earlier. These numerous correlations provide strong evidence that species are active earlier in the spring due to warming climate. A total of 22 of the 24 species showed a trend toward earlier activity with warmer temperatures, more than expected by chance ($\chi^2 = 16.7$, $df = 1$, $P < 0.001$).

DISCUSSION

Using the observations of a Middleborough naturalist from 1970 to 2002, we were able to

demonstrate that most phenological events in an assemblage of 24 species are now occurring earlier than they were 33 years ago, with 5 species showing significant trends. This trend was most strongly represented by the arrival time of birds in the spring. Further, we were able to show that spring phenological events are related to increasing springtime temperatures during this time period (a significant relationship for four species), affecting birds, plants, amphibians, and butterflies.

As might be expected, there was variation in statistical significance among species, which could be due to different behaviors or population dynamics of birds, plants, insects, and amphibians. For instance, migratory birds come to the farm from different wintering lo-

calities, which may mean that they respond to temperatures other than those in Middleborough (Mason 1995, Both and Visser 2001). Environmental changes that affect bird migration may occur where the birds overwinter or along their migration routes (Huin and Sparks 1998, 2000; Cotton 2003). In particular, the direction and intensity of the wind might facilitate or retard the arrival times of spring migrants. Therefore, weather changes in Middleborough itself may not play the dominant role in the timing of bird arrivals for certain species. Conversely, the first arrival of Wood Ducks is closely tied to the spring ice-melt in one pond on the farm (K. S. Anderson pers. comm.), a truly local weather effect. The three other species whose phenology was significantly related to temperature were also wetland or moist woodland species—Red-winged Blackbird, goldthread, and spring peeper—indicating the importance of warm temperatures in facilitating early activity in wet and moist areas.

Fluctuations in population size could affect first observations of phenological events: decreases may cause first observations of migrants (or blooms, appearances, calls, etc.) to occur later, masking the actual trend of birds migrating earlier (Sparks 1999, Tryjanowski and Sparks 2001). For example, observations from the Manomet Center for Conservation Sciences, located 28 km east of the Middleborough farm, revealed that populations of several of the bird species we studied have decreased over time (Hagan et al. 1992, Lloyd-Evans and Atwood 2004). Populations of Wood Thrush (*Hylocichla mustelina*), Gray Catbird (*Dumetella carolinensis*), Yellow Warbler (*Dendroica petechia*), Black-and-white Warbler, Ovenbird, and Baltimore Oriole (*Icterus galbula*) declined significantly over the past 30 years, whereas Hermit Thrush (*Catharus guttatus*) populations did not change. None of the species common to our study and the Manomet studies was shown to increase in population over the past 30 years (Lloyd-Evans and Atwood 2004).

Finally, migratory patterns of some avian species are based upon endogenous rhythms that are not affected by climate (Gwinner 1996). In the case of plants, butterflies, and amphibians, there were correlations of early spring activity with increasing spring temper-

atures. Since all of those species are permanent residents of Middleborough, they are affected more by increasing temperatures in that area.

When we examined the patterns of arrival times in other locations in North America, we found no consistent pattern of response to climate change. For example, the first House Wrens, which we found to arrive significantly earlier over time, also have been arriving significantly earlier in Wisconsin (Bradley et al. 1999) and New York, but not elsewhere in Massachusetts (Butler 2003). We found that the first Wood Thrushes were not arriving significantly earlier, a finding that agrees with results from Wisconsin (Bradley et al. 1999), but runs counter to findings in New York and Massachusetts (Butler 2003). Despite the inconsistencies between studies, the signs (positive or negative) of our regression results for the change in first arrival over time agreed with those of other studies of the same species (Bradley et al. 1999, Butler 2003). That is to say, when we found evidence for earlier arrival of species (significantly or not) over time—which we found for all species except Black-and-white Warbler and Common Grackle—so did other studies for that species. It also is worth noting that Butler (2003) found that the first Black-and-white Warblers were arriving later over time in Worcester County, Massachusetts, albeit not significantly, just as we did. This apparently anomalous finding simply could be due to the decline of Black-and-white Warbler populations in the Northeast (Lloyd-Evans and Atwood 2004).

We were able to use the observations of a naturalist to demonstrate that some phenological events are occurring earlier over time and as temperatures increase. Because Mrs. Anderson did not anticipate scientific use of her observations (presumably, much like most other naturalists), use of her data presented challenges. Most significantly, irregularities in her collection of data (see Methods) likely resulted in unintended variation in the data, possibly obscuring biologically significant trends. In her case, however, the relatively small number of gaps in her observations still allowed us to discern clear evidence of biological response to climate change.

This private journal of observations from 1970 to 2002 has proven to be a sufficiently

accurate and long-term data source for climate warming research, demonstrating clear patterns of earlier phenological events. We believe that there are large numbers of such journals and records, and these could be valuable for illustrating the impact of climate change in many regions of the world, particularly those areas for which there are no long-term records collected by scientists and research organizations. Some of these records may not have data of high-enough quality to demonstrate biological patterns, particularly where species identifications are uncertain, observations are made irregularly, or sampling intensity changes over the course of time. However, where high-quality records exist, they could extend our knowledge of plant and animal distributions, and help us determine how the changing climate has already affected biological communities and how such communities are likely to react to further climate change. Biologists interested in climate change research should actively seek out such records, analyze them, and present their results to the scientific community.

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HOME RANGE AND HABITAT USE BY AMERICAN CROWS IN RELATION TO TRANSMISSION OF WEST NILE VIRUS

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ABSTRACT.—Determining the sizes and characteristics of home ranges among American Crows (*Corvus brachyrhynchos*) in spring/summer is essential for understanding the importance of this species in the transmission of West Nile virus. In late spring, summer, and early fall of 2002, we radio-tracked 45 American Crows to estimate their movements and habitat preferences in urban and adjacent agricultural habitats in east-central Illinois. The 95% minimum convex polygon home ranges averaged 9.6, 6.7, and 6.4 km² for hatch-year, sub-adult, and adult crows, respectively. Proportional habitat use was investigated at two scales: (a) at the study site scale, there was a preference for low- to medium-density urban habitat and avoidance of forested habitat; and (b) at the home range scale, there was a preference for agricultural cover and avoidance of high-density urban habitat. Received 16 October 2003, accepted 19 July 2004.

Corvid populations are increasing worldwide in response to urbanization (Marzluff et al. 2001), and the American Crow (*Corvus brachyrhynchos*) is a successful exploiter of human environments in North America. Home-range estimates for crows are distinct in different geographic settings, and range from 0.01 km² in highly urban environments to over 35 km² in non-urban landscapes (Marzluff et al. 2001). A number of studies (reviewed by Verbeek and Caffrey 2002) have contributed to our understanding of spatial and geographic area requirements of crows. During winter, Stouffer and Caccamise (1991) captured crows on agricultural fields in New Jersey and divided them into two groups: diurnal, activity-center based (DAC) crows and vagrant crows. DAC crows used daytime territories ranging in size from 0.3 to 0.5 km² and returned to the communal feeding area nearly every day. Vagrants could be found during only 31.8% of daytime tracking attempts; crows of both groups roosted together at night. McGowan (2001) found that suburban crows in New York defended 0.09 km² territories, whereas their rural counterparts de-

fended 0.4 km² territories in the spring. Sullivan and Dinsmore (1992) determined that, during the breeding season, home-range size for 10 pairs of crows in Manitoba was 2.6 km².

The prevalence of vector-borne disease is often related to the home-range size, habitat availability, and habitat selection of host species. The American Crow is a reservoir host for the mosquito-transmitted West Nile virus (WNV; McLean et al. 2001). The birds attain a high blood viral titer before death (McLean et al. 2001) and may serve as amplifying hosts, increasing local transmission. Dead, WNV-positive crows may serve as effective sentinels of local transmission (Nasci et al. 2002, Guptill et al. 2003). To date, there has been little study of movement and habitat use by crows in urban areas during the period when the risk of transmitting WNV is high. Knowledge of home-range size, the geographic area over which an infected crow may potentially move, and habitat composition are essential for understanding how crows relate to transmission foci for WNV.

Our study of crows in a Midwestern urbanized setting with adjacent agricultural lands was designed to (1) estimate home-range sizes of crows during the late spring through early fall season, (2) describe habitat use, and (3) relate our findings to the potential for WNV transmission by this species.

METHODS

From February through October 2002, we captured crows on communal feeding grounds

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with Australian crow traps (Kalmbach and Aldous 1940, Rowley 1968) within 1.6 km of the South Farms agricultural property (40° 2' N, 88° 17' W) of the University of Illinois in Urbana-Champaign, Illinois. Crows were aged by palate coloration and plumage characteristics (Pyle 1997) as hatch-year, sub-adult (year-old individual), or adult (second year and older). We weighed, measured, and banded birds at capture, and determined their gender by discriminant analysis of external measurements. Using a sample of known-sex individuals, we used age-group-specific discriminant functions to determine gender. A series of eight mensural characters were evaluated for use in discriminant analysis, including bill length, width, and depth; head-to-bill length; length of wing chord, tail, and tarsus; and mass. The performance of each function was evaluated through cross validation, yielding 94, 100, and 78% correct classification for hatch-year, sub-adult, and adult crows, respectively (Yaremych et al. 2004a).

Radio-transmitters were attached to a subsample ($n = 56$) of captured crows. Radio-transmitters were custom designed (by W. Cochran, Champaign, Illinois), and weighed <2 g for tail-mount, and <3 g for collar-mount. Transmitters had an expected battery life of approximately 6 months. We used a tail-mount attachment most frequently ($n = 46$), modifying the method of application of Dunstan (1973). Attachment was to the rachis of the central tail feather. The back of the transmitter and battery were lined with epoxy and laid on top of the central tail feather shaft, with the transmitter roughly 2.5 cm below the uropygial gland. We used a needle and thread to stitch through the rachis under the transmitter, and wrapped thread repeatedly around the transmitter and battery and under the tail feather. Five additional stitches were used to secure the antenna to the rachis; the antenna ended at the distal tip of the tail feather. All sutures were coated with epoxy to protect them from weathering. Alternatively, collar-mount transmitters were attached to crows caught before molting ($n = 10$). Collars were individually adjusted for optimal sizing and sewn around the necks of crows.

Each radio-tagged crow was tracked using vehicle-mounted twin Yagi antennas to obtain locations approximately 10 times per week

(Cochran 1980). Tracking was stratified equally between morning (06:00–12:00 CST), afternoon (12:00–20:00), and nighttime (20:00–06:00). We searched for birds that we were unable to locate while on foot or by vehicle with fixed-wing aircraft. Point locations, taken with Global Positioning Systems (GPS; Garmin GPSIII), were used for analysis of home range. All GPS locations were recorded while crows were on the ground or in trees. Typically, the minimum number of radio-locations required to yield a stable home-range size was 10, and home-range size was not estimated for crows that were located <10 times. Radio-tracking efforts for the remaining crows declined after 31 October.

Any crow that was encountered dead was tested for West Nile virus using immunohistochemical staining (Heinz-Taheny et al. 2004) at the University of Illinois College of Veterinary Medicine, or TaqMan reverse transcriptase–polymerase chain reaction (Lanciotti et al. 2000) at the Medical Entomology laboratory at the Illinois Natural History Survey.

Locations were plotted on the 1999–2000 satellite imagery of Illinois Land Cover (Illinois Interagency Landscape Classification Project 2003) using a Geographical Information System (Environmental Systems Research Institute 1998). The 95% minimum convex polygon (MCP) estimator for home range was used to describe the outer limits of each crow's movement (Mohr 1947). Additionally, adaptive kernel (ADK) home ranges were computed at the 50 and 95% contour levels (Worton 1989) for identification of activity centers.

We defined the study site as the cumulative area used by all the radio-tracked crows in spring through early fall; this area is the merged 95% MCP home ranges for the 45 crows included in the study. The study site, totaling 39,471 ha, encompassed the cities of Champaign and Urbana, as well as the surrounding agricultural areas. We delineated and categorized the cover types on the site as (a) agriculture—primarily corn, soybeans, winter wheat, and rural grassland and residences; (b) forest—areas predominantly covered with trees and woody vegetation, including upland deciduous closed-canopy forests, upland open-canopy/savannah forests, and closed-canopy floodplain forests situated in lowlands

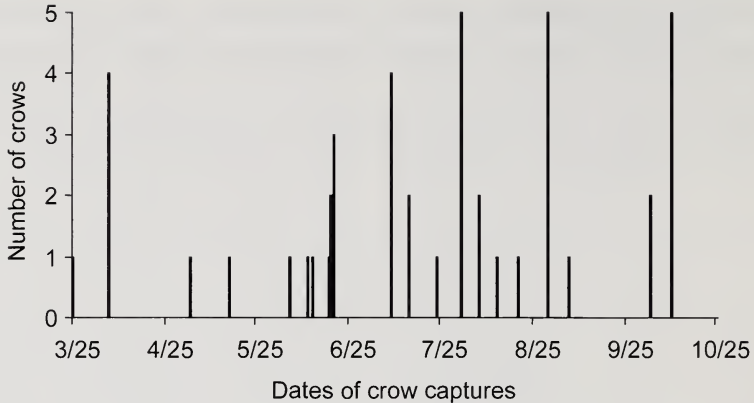


FIG. 1. Capture dates of 45 American Crows used for analysis of home range and habitat use in east-central Illinois, late spring through fall, 2002.

and temporarily flooded floodplains; (c) high-density urban—all or nearly all of the land surface covered with manmade structures; (d) low- to medium-density urban—up to 50% of the land surface covered with manmade structures; and (e) urban open space—including parks, golf courses, cemeteries, and other grassland-like cover within urban and built-up areas intermixed with other cover, such as forest. Each telemetry location was buffered (25 m) to account for telemetry error.

Habitat use was interpreted by compositional analysis (Aebischer et al. 1993) at two scales of analysis using Resource Selection software (Leban 1999). Compositional analysis examines habitat use, with each animal, not each location, serving as the sampling unit, thereby avoiding potential autocorrelation problems often associated with radio-telemetry studies (Aebischer et al. 1993). First, the relative amount of habitat within each crow's 95% MCP home range was compared to the relative amount of each habitat available within the total study site for analysis at the study site level. Second, the habitat of telemetry locations (the habitat a crow was using when we recorded a telemetry location) was compared with the relative amounts of each habitat within an individual's MCP home range for analysis at the home-range level.

The values (%) representing habitat use and availability were log-ratio transformed as part of the analysis. Resource Selection software replaced the 0% value for those habitat types that were not utilized, yet available, with

0.001% to allow for this transformation. Where there is significant nonrandom use (i.e., habitat use within the site or home range differed significantly from use at random, as determined with Resource Selection), the habitat types can be ranked in order of increasing relative use. If a habitat type was used more than expected based on its availability, it was considered to be preferred; habitats were ranked from least preferred (0) to most preferred (4; Aebischer et al. 1993). Selection index graphs were created based on pairwise comparisons of means of the log-ratios of habitat use.

RESULTS

From February through October 2002, we captured 156 crows, 56 of which were fitted with a radio-transmitter. Due to death, missing signals, or radio-transmitter failure, only 45 of the radio-tagged crows remained in the study long enough for us to acquire a sufficient number of radio-locations to achieve stability in home-range estimates. Captures of these 45 crows took place from 25 March to 10 October, with 80% of the captures occurring after mid-June (Fig. 1). This sample was composed of individuals from the various age and sex categories as follows: 26 hatch-year females, 7 hatch-year males, 3 sub-adult females, 4 sub-adult males, 4 adult females, and 1 adult male. The number of locations obtained for all crows was 2,147, with an average number of 48 locations per crow.

During our study, 68% of radio-tracked crows died and tested positive for WNV (in-

cluding some crows for which home ranges were not estimated due to a lack of sufficient number of locations; Yaremych et al. 2004b). Observations of 10 infected crows 1 to 2 days before death indicated a change in their normal movement patterns. For example, three sick crows either did not return to a nighttime roost from the communal feeding area in the afternoon, or did not fly to the feeding area from the roost in the morning. Instead, these crows were found alone between the day and nighttime areas, and they did not feed. One crow was perched in a tree with one eye closed. Other crows were found on the ground and did not move as we approached, and were found dead later that day or the next morning. We removed the last-location data points (crows not moving) before computing home ranges for the crows that we tracked immediately before the death due to WNV. Accordingly, our analysis represents the movement and habitat use of crows displaying normal movement patterns. In many situations, a crow was located at a regular roost at night, and by the next tracking session (1–2 days later), the crow was found dead in urban habitat near the roost; thus, there were no observations indicating that the crow was sick.

The 95% minimum convex polygon home-range sizes for hatch-year, sub-adult, and adult crows averaged 9.6, 6.7, and 6.4 km², respectively. The 50% (core area) and 95% adaptive kernel home-range sizes were hatch-year crows: 2.3 and 14.4 km²; sub-adults: 1.1 and 6.9 km²; and adults: 1.1 and 6.1 km², respectively. Home-range size did not differ significantly between sexes (Mann-Whitney U -test = 154, $df = 1$, $P = 0.44$), or among age classes (Kruskal-Wallis H -test = 2.47, $df = 2$, $P = 0.25$). The average minimum convex polygon home-range size across sexes and age classes was 7.6 km². Home ranges of crows overlapped extensively. Crows were frequently located during the day in agricultural habitat south of the residential area where they roosted. The agricultural habitat was a communal feeding area, and crows of many family groups fed there for the duration of spring-to-fall tracking.

The study site was composed of 38% agriculture, 30% low- to medium-density urban, 22% high-density urban, 5% forest, and 5% urban open space. Habitat use within the study

site (all ages and sex classes) differed significantly from random ($P < 0.001$); i.e., crows established home ranges in a non-random manner. Habitat use within home ranges also differed from random ($P < 0.001$). In the study site analysis (home range versus study site), crows preferred low-density urban areas and tended to avoid the more forested areas; in the home-range analysis (locations versus home range), crows preferred agricultural cover and tended to avoid high-density urban areas (Fig. 2). Resource ranking matrices, which rank the cover types according to relative use (highest-ranking habitat is most preferred) were (1) study site analysis ($P < 0.001$): forest = 0, agriculture = 1, high-density urban = 2, urban open space = 3, low-density urban = 4; (2) home-range analysis ($P < 0.001$): high-density urban = 0, urban open space = 1, forest = 2, low-density urban = 3, agriculture = 4. Crows of all age classes demonstrated a general pattern of foraging in agricultural areas during the daytime and roosting in urban areas at night. All crows in this study were captured in the agricultural areas and all roosted in the adjacent urban areas, with fidelity to one or two preferred roosts and occasional travel to other urban roosts.

When comparing age classes for habitat composition of home ranges, adults used more forest (13.0%) than both hatch-year crows (5.5%; $U = 145$, $df = 1$, $P = 0.004$) and sub-adult crows (6.0%; $U = 28.5$, $df = 1$, $P = 0.044$). For each of the five habitats, no differences ($U = 160$ – 254 , $df = 1$, $P = 0.079$ – 0.488) were detected in habitat composition of the home ranges used by males and females. Habitat composition of telemetry locations was different among age classes for low- to medium-density urban habitat only ($H = 6.58$, $df = 2$, $P = 0.038$): sub-adults used this habitat more than hatch-year crows ($U = 181.5$, $df = 1$, $P = 0.010$) or adult crows ($U = 6$, $df = 1$, $P = 0.037$). Habitat composition at telemetry location sites differed between sexes: females used agriculture ($U = 102$, $df = 1$, $P = 0.007$) and forest ($U = 130$, $df = 1$, $P = 0.042$) more than males, and males used high-density urban habitat ($U = 268.5$, $df = 1$, $P = 0.036$) and low- to medium-density urban habitat more ($U = 304$, $df = 1$, $P = 0.003$) than females.

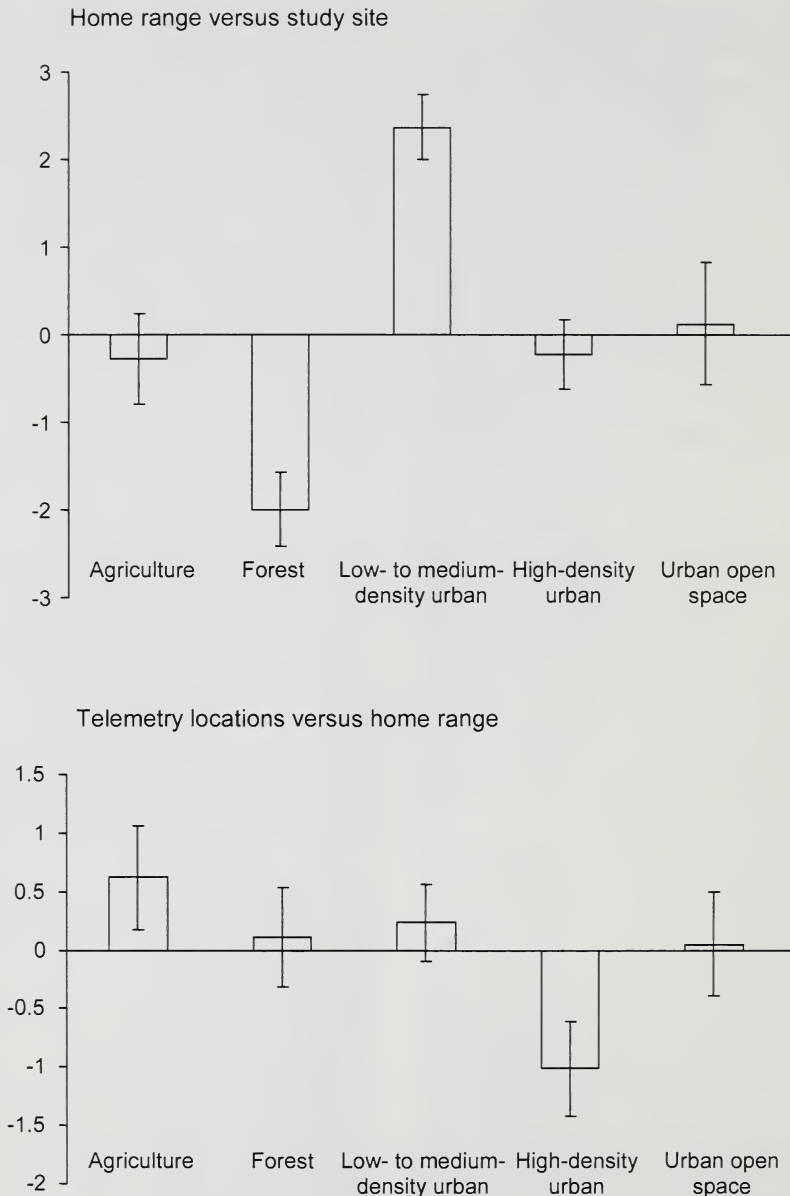


FIG. 2. Habitat selection indices at the scales of study site and home range for American Crows in east-central Illinois, late spring through fall, 2002. Positive values indicate selection, and negative values indicate avoidance. Bars show log-ratio means of habitat selection for crows. Error bars are \pm SE.

DISCUSSION

Our data afford a general picture of where crows spend time during late spring through fall, and are of timely interest in defining the potential role of crows in the spread of WNV. After beginning to feed on their own, young crows appeared to enter the traps on the com-

munal feeding areas more readily than the older crows, perhaps because younger birds are less experienced. The result is an age bias in our sample toward hatch-year crows. Home ranges were constructed for the cumulative season of late March through the end of October, with most crows entering the study in

mid-June and later, and crows exiting the study throughout. The majority of the captures before mid-June were sub-adult and adult crows, whereas the majority of captures in late June and later were hatch-year birds. The differences in habitat use among age classes may relate to the temporal bias in our sampling, with adults possibly using more forest in the early portion of the study because many nested in forest. As a majority of crows were captured in mid-June and later, our study does not focus on home ranges of breeding crows. In east-central Illinois, crows mate in late February and early March, and a majority of young crows have left the nest by May (Grabner et al. 1987). The crows of Urbana-Champaign had larger home ranges compared with those of crows studied in New Jersey, New York, and Manitoba (Stouffer and Caccamise 1991, Sullivan and Dinsmore 1992, McGowan 2001). Some of the variation among studies is due to differences in how area use was measured (defended territories in New York; complete 95% home ranges in Urbana-Champaign; Marzluff et al. 2001), seasonality (mid-April through mid-July in Manitoba; locations taken through the fall in Urbana-Champaign), and time periods (daytime home ranges in New Jersey; combined daytime plus nighttime home ranges in Urbana-Champaign).

That home-range sizes of crows did not differ among age classes may be a result of small sample sizes for the older age classes in the late season. As several crows entered the study in September and October, location data contributed by these birds to the overall home-range and habitat-use estimates were for the later months only. Accordingly, individuals captured early in the study, but which died before the study ended, contributed only early season data. We note that the general movement patterns of the crows did not differ throughout the study period: in general, all crows were captured in agricultural feeding areas, these feeding areas were used throughout the entire tracking season, most crows roosted in urban areas, and the same urban roosts were used continually throughout the tracking season.

Crows selected low- to medium-density urban cover and tended to avoid the more forested areas. Differential habitat use may be related to diet (Marzluff et al. 2001). The ur-

ban environment may provide food sources to supplement agricultural foraging, resulting in a diminishing need for forest food resources. The juxtaposition of urban and agricultural habitat within our study site may facilitate the exploitation of abundant and easily located anthropogenic food resources in the agricultural and urban areas. While in the agricultural setting, crows tended to be found feeding in the fields that were most recently tilled or harvested to exploit recently uncovered invertebrates and waste grains. While in the urban setting, crows commonly fed from dumpsters and were found in picnic areas and parking lots. The preference of crows for low- to medium-density urban cover may expose crows to the primary vector of WNV in Illinois, the urban-dwelling *Culex pipiens* (Foster and Walker 2002).

The period of our study on crow movement and habitat use overlapped the mosquito season, thus representing the WNV transmission season. The high mobility of crows underscores the potential importance of this species in the transmission of WNV over a large spatial area, although the movement of infected crows in nature is difficult to study because the exact time of exposure of crows to WNV is unknown. The general daily pattern of feeding in agricultural cover and roosting in urban cover is evidence for potential movement of WNV between two distinct habitats if crows carry the virus between habitats and if mosquitoes feed upon birds in both areas.

In laboratory settings, crows die of WNV within 4–7 days post-infection (McLean et al. 2001, Komar et al. 2003), and are sufficiently viremic to infect a feeding mosquito for 3–5 days before death (Komar et al. 2003). Our field observations of sedentary, defenseless behavior in WNV-positive crows 1–2 days before death suggest that an infected crow may provide an easy blood meal for bird-feeding mosquitoes, and crows may serve as reservoirs for WNV transmission. Our observations that crows became notably disabled only for a short time (reduced movement 1–2 days before death) suggest that crows may travel to regular communal feeding areas and roosts while infected and transport WNV across an average home-range size of 7.6 km².

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A COMPARISON OF TECHNIQUES FOR MARKING PASSERINE NESTLINGS

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ABSTRACT.—We examined eight marking techniques designed specifically for use on newly hatched Red-winged Blackbird (*Agelaius phoeniceus*) nestlings (colored polishes applied to either the culmen or the hallux; colored elastic, plastic, or band-aid bands applied to the tarsus; stains applied to either the superciliary down or the tarsus; and superciliary down clipping) to determine which technique had the shortest application time and longest retention. Application times and retention rates varied between marking techniques, but this did not affect nestling growth or survival. Clipping of superciliary down feathers had the shortest application time and the highest retention rate of all techniques studied. This technique, however, is only applicable to species whose newly hatched young have superciliary down. Other techniques examined had comparably short application times, but were not retained for the entire nestling period. Received 19 March 2004, accepted 31 August 2004.

Adult birds are marked for individual identification by various techniques, including attachment of patagial tags (Brua 1998), nasal saddles (Koob 1981), plastic neckbands (Helm 1955), and aluminum or colored leg bands (Marion and Shamis 1977). However, such techniques are often not suitable for marking young birds because of their rapid change in body size as they grow. Nonetheless, it is often necessary to identify individual nestlings when studying nestling growth rates (Degen et al. 1992), begging behavior (Bachman and Chappell 1998, Saino et al. 2001), survival rates (Howe 1976), or the effects of human disturbance (Davis and Parsons 1991, Fernandez 1993).

Only a few techniques exist for the sole purpose of identifying passerine nestlings, such as colored plastic bands (Harper and Neill 1990), band-aids or plastic tape (Downing and Marshall 1959), threads tied around the tarsus (Oniki 1981), colored dyes or ink (Redondo and Castro 1992), and colored nail polish applied to the hallux (Holcomb and Twiest 1971). As with many techniques, Holcomb and Twiest (1971) found that nail polish required reapplication every 2 days during the nestling period to ensure identification of individuals. Other marking techniques, such as India ink tattoo marking on the abdomen (Ricklefs 1973) and clipping toenails (St. Lou-

is et al. 1989), do not require reapplication throughout the nestling period, but they are often difficult to apply or expensive to use [e.g., passive integrated transponders (P.I.T.) tags; Carver et al. 1999]. Marking techniques that require frequent reapplication or that have a long application time may result in increased nest disturbance. For some nidicolous species [e.g., Northern Harriers (*Circus cyaneus*)], even low levels of human disturbance can reduce parental care, increase parental alarm calls, increase nestling blood urea levels, and decrease the number of feeding trips by parents (Fernandez 1993). Furthermore, nest visitation by humans may also increase total nest mortality by predation (Bart 1984) because the nest is unguarded for some time until the parent returns.

An ideal marking technique for passerine nestlings would be inexpensive, readily available to researchers, have a short application time, and maintain its color or visibility for the duration of the nestling period. Based on these criteria, the primary objective of our research was to determine which of the following marking techniques was best suited for marking Red-winged Blackbird (*Agelaius phoeniceus*) nestlings: (1) nail polish applied to the hallux; (2) nail polish applied to the culmen; (3) colored plastic bands applied to the tarsus; (4) colored elastic bands applied to the tarsus; (5) colored band-aids applied to the tarsus; (6) stains applied to the superciliary down; (7) stains applied to the skin; or (8) superciliary down clipping. Our secondary objective was to determine whether marker application time or the type of identification

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marker used affected nestling growth or survival rates prior to fledging.

METHODS

We conducted our study during May through July, 2001–2002, in eastern and southern Ontario. We searched for Red-winged Blackbird nests every other day within the emergent vegetation around wetlands near the towns of Arnprior (45° 26' N, 76° 21' W), and Long Point (42° 34' N, 80° 25' W). Nests were marked and numbered using inconspicuous flagging tape placed approximately 2 m from the nest. During late incubation, Red-winged Blackbird nests were checked daily for newly hatched (<24 hr old) nestlings. Each nestling in a brood was marked with a different technique chosen at random with the constraint that, for most nests, one nestling from each brood would be marked with nail polish applied to the hallux (for other research activities). For Red-winged Blackbird clutches that hatched asynchronously, nests were visited at least once daily during the hatching period, so that each last-hatched nestling could be marked within 24 hr of hatching.

Marking techniques.—The nail polish technique was divided into two methods, based on the appendage being marked: either the nail of the hallux (hereafter referred to as hallux), or the upper mandible. Revlon Top Speed 60-sec quick drying nail polishes in red (beet), purple (eggplant), and brown (mocha) were used because these colors were easily distinguishable from one another and from the hallux of nestlings. Application of nail polish to the hallux required a nestling to be inverted in the palm of one hand while using the other hand to apply polish to the entire hallux with the polish applicator. The polish was allowed to dry for 60 sec before the marked nestling was returned to the nest. Returning a nestling to the nest before the polish was completely dry sometimes resulted in the nestling's digits becoming stuck together. These same polish colors and methods were used to apply nail polish to the nestling's upper mandible. Using the applicator, a stripe of polish was applied from just below the nares to the tip of the mandible.

The colored leg band technique was divided into three methods, based on material used:

colored plastic, colored elastics, or colored band-aids. Plastic leg bands were modified from decorative colored beads, and were cut so that they were 3 mm in diameter and 1 mm in length. Each band, the color of which was chosen at random, was placed on a bander's shoehorn, and then slipped over the tarsus. Because the bands were opened lengthwise, it was assumed that they would expand as the nestling's tarsus grew. Elastic bands used for tightening tooth braces and readily available from dental offices were also used to mark Red-winged Blackbird nestlings. Applying elastic bands required the band to be opened slightly, usually with tweezers, and then slipped over the digits to the proximal end of the tarsus. The band-aid band was modified from Johnson & Johnson's miniature band-aids that had been cut lengthwise into two equal pieces (5 × 35 mm). To apply the band-aid leg band, the cotton center of the band-aid was placed around the tarsus and then the two adhesive ends were connected to create a snug fit around the tarsus. The excess adhesive ends were trimmed nearly flush with the tarsus.

The staining technique was divided into two methods, based on the location being marked: either the superciliary down feathers (eyebrow stripe) or the skin of the tarsus. Using an eyedropper, one drop of blue drawing ink was placed directly on the superciliary down feathers and brushed through the down with a small paintbrush. Care was taken not to allow ink to get into the nestling's eyes. The stain was then allowed to dry (~1 min) before the nestling was returned to the nest. Other nestlings were marked by applying a drop of ink to the tibio-tarsal joint (heel), brushing it evenly over the skin with a small paintbrush, and then allowing it to dry completely (~1 min) before the nestling was returned to the nest.

The final technique used to mark Red-winged Blackbird nestlings was superciliary down clipping. Once nestlings were immobilized, fine scissors were used to trim one half (either front half or back half) of either the right or left superciliary down stripe, producing four unique markings.

Methods of assessment.—The time (± 1 sec) to apply a marker was recorded from the moment the nestling had settled in the hand until

the marker was dry, securely fastened to the tarsus, or the superciliary down was cut.

After initial application of markers to newly hatched nestlings, nests were revisited every other day to assess the markers. In Ontario, nestlings usually fledge when they are 10–11 days old, but may leave their nests prematurely if they are handled after 8 days of age. Thus, we did not assess markers beyond the 9th day of the nestling period; if a marker was still present at day 9, we recorded it as “present at fledging.” Percent and/or intensity of polishes and stains present was assessed subjectively, based on the amount of original marker remaining on the nestling. To minimize bias, we devised a scoring system for recording percentages. When the percentage of marker remaining fell below 10% (i.e., barely visible), nestlings were remarked. If, during the nestling period, leg bands fell off or were missing, the same band type was re-applied. If a marker had to be reapplied, and the nestling survived until fledging, the marker was scored as not present at fledging (day 9).

Growth rates.—Many studies of nestling performance have measured nestling growth as the daily change in mass from hatching until fledging (e.g., Quinney et al. 1986). To determine whether marking techniques affected nestling growth, newly hatched, marked nestlings were weighed (± 0.01 g) using a digital scale. Time of day when nestlings hatched was estimated (± 6 hr) based on their size and on the state (wet or dry) of their natal down. When surviving nestlings were 8 days old, they were reweighed (± 0.01 g). Last-hatched nestlings from asynchronously hatching broods were remeasured the day after their older siblings were measured. These data were used to calculate nestling growth rates. The fate of nestlings and all incidences of nestling injury, disappearance, or death were recorded. A nestling was recorded as fledged if it survived to 9 days of age.

Statistical analyses.—One-way ANOVA was used to determine whether initial marker application time and nestling growth rate differed among marking techniques. When significant differences were found ($P \leq 0.05$), post-hoc comparisons were conducted using Tukey's test. Using the Mayfield method (Mayfield 1961, 1975), we calculated daily

survival rates of nestlings for each marking technique. The Mayfield daily survival rate is the probability that nestlings will survive until the next day. Similarly, for each marking technique, we calculated the probability that the marker would be retained until the next day. Standard errors for Mayfield estimates were calculated using methods described by Johnson (1979). We used chi-square analysis to determine whether the number of nestlings that survived to fledging differed among marking techniques. A chi-square analysis was also used to determine whether the number of markers present at fledging differed among treatments. Results for all statistical analyses were considered significant at $P \leq 0.05$. Means are reported \pm SE.

RESULTS

We found 114 Red-winged Blackbird nests and marked 338 newly hatched nestlings. Of nests from which at least one young fledged ($n = 46$ nests), partial brood loss ($n = 20$ nests) was usually attributable to starvation of the last-hatched young. Complete brood loss ($n = 68$ broods) was always the result of predation.

Mean application times of markers ranged from 20–145 sec (Table 1). Colored elastic bands (mean = 145.3 ± 20.3 sec) and band-aid bands (mean = 137.4 ± 19.6 sec) applied to the tarsus had the longest application times, whereas superciliary down clipping (mean = 19.7 ± 2.2 sec) had the shortest application time. Growth rate of nestlings did not differ ($F_{7,109} = 0.82$, $P = 0.58$; Table 1) between any of the marking techniques. However, nestlings marked with stains applied to the superciliary down had the slowest growth rate (3.6 ± 0.5 g/day) and nestlings marked with elastic bands applied to the tarsus had the fastest growth rate (4.4 ± 0.6 g/day). The proportion of nestlings that fledged did not differ among the eight marking techniques ($\chi^2 = 10.1$, $df = 7$, $P = 0.18$; Table 1). Daily nestling survival rate was highest for the superciliary down clipping technique (0.95 ± 0.02) and lowest (0.88 ± 0.02) for polish applied to the culmen. Marker retention (markers present at fledging, or 9 days of age) differed among techniques ($\chi^2 = 71.5$, $df = 7$, $P < 0.001$; Table 1). Daily marker retention rates were highest for nestlings marked with superciliary down clipping

TABLE 1. Number of Red-winged Blackbird (*Agelaius phoeniceus*) nestlings marked, mean application time (\pm SE) of marker type, growth rate (\pm SE) of nestlings, number of nestlings fledged (those surviving to day 9), daily nestling survival rate (\pm SE), number of markers present at fledging (i.e., those present at day 9), and daily marker retention rate (\pm SE) for each marking technique. Data are from eastern and southern Ontario, 2001–2002.

Technique	Nestlings marked (n)	Mean application time (sec)	Growth rate (g/day)	Nestlings fledged (n)	Daily nestling survival	Markers present at fledging (n)	Daily marker retention
Polishes							
Culmen	36	70.7 \pm 3.4 C ^a	4.3 \pm 0.4	10	0.88 \pm 0.02	3	0.80 \pm 0.03
Hallux	96	69.0 \pm 4.0 C	4.1 \pm 0.6	34	0.91 \pm 0.01	0	0.75 \pm 0.02
Leg bands							
Plastic	55	60.3 \pm 4.6 B	4.0 \pm 0.4	19	0.90 \pm 0.02	7	0.85 \pm 0.02
Elastic	36	145.3 \pm 20.3 D	4.4 \pm 0.6	9	0.89 \pm 0.02	7	0.88 \pm 0.02
Band-aid	28	137.4 \pm 19.6 D	3.7 \pm 0.3	8	0.89 \pm 0.02	2	0.82 \pm 0.03
Stains							
Superciliary	28	74.3 \pm 3.1 C	3.6 \pm 0.5	9	0.90 \pm 0.02	8	0.89 \pm 0.02
Tarsus	34	75.7 \pm 3.9 C	3.8 \pm 0.4	13	0.92 \pm 0.02	0	0.76 \pm 0.04
Clipping							
Superciliary	25	19.7 \pm 2.2 A	4.0 \pm 0.4	15	0.95 \pm 0.02	15	0.95 \pm 0.02
		$P < 0.001^b$	$P = 0.58^b$	$P = 0.18^c$		$P < 0.001^c$	

^a Mean application times followed by the same letter were not significantly different ($P > 0.05$) from one another in pairwise post-hoc comparisons (Tukey's test).

^b One-way ANOVA.

^c Chi-square test, $df = 7$.

(0.95 \pm 0.02) and for blue ink applied to superciliary down feathers (0.89 \pm 0.02). Polishes applied to the hallux and ink applied to the tibio-tarsal joint had the lowest daily marker retention rates (0.75 \pm 0.02 and 0.76 \pm 0.04, respectively) and never lasted until fledging unless they were reapplied.

DISCUSSION

Of the techniques examined in our study, superciliary down clipping had the shortest application time of any marker used and was readily visible for the entire nestling period. This technique is ideal for marking Red-winged Blackbird nestlings because capital tract feathers are the last to project through the epidermis of the cranium (Holcomb and Twiest 1971); consequently, the white superciliary down feathers are present throughout the nestling period. Interestingly, few studies have reported using this technique for marking nestlings. Magrath (1991) marked nestling Blackbirds (*Turdus merula*) by clipping specific tufts of down to allow individual recognition. Of course, this technique is only applicable for species whose nestlings have superciliary down at hatch.

Although there was considerable variation in application times of marking techniques, growth rates and survival of nestlings did not differ among techniques. This suggests that the human disturbance associated with applying markers had no adverse effects on growth or survival of Red-winged Blackbird nestlings (St. Louis et al. 1989). However, several marking techniques were found to be potentially harmful to nestlings. Nestlings marked with stain on the superciliary down, for example, often retained the marker until fledging, but five marked chicks were found with their superciliary down missing (along with their colored stain), leaving the nestlings bald. Hamel (1974) observed a high incidence of color-marked Common Grackle (*Quiscalus quiscula*) nestlings being maimed by the parent birds' attempts to dispose of the colored markers. Oniki (1981) suggested that colored threads used to mark nestling Slaty Antshrikes (*Thamnophilus punctatus*) were pecked at or pulled off by adults who peer into the nest before and during brooding. Hence, we assumed that the brooding parents pulled out the nestlings' colored down. Growth rates of nestlings marked with this technique did not differ

statistically from other marking techniques, but nestlings did grow 0.3 g/day slower compared with the mean growth rate of all other techniques combined. We are uncertain, however, whether the slow growth rates were due to decreased parental brooding, presence of stain, or loss of nestling down. Because there is a strong positive relationship between fledging weight and juvenile survival (Garnett 1981, Magrath 1991, Keller and Van Noordwijk 1993), staining nestlings' superciliary down is not recommended for any nestling studies, especially research on endangered or threatened species.

Colored plastic bands applied to the tarsus of nestlings also occasionally caused superficial injuries to nestlings. On four occasions when chicks were remeasured 8 days after hatching, the colored plastic leg band left an indentation in the leg where the band had rested. All nestlings maintained grasping abilities, but it was not possible to determine whether there were any chronic effects. Harper and Neill (1990) also reported band related injuries (two broken tarsometatarsi and one broken hallux) due to colored plastic bands applied to nestling House Wrens (*Troglodytes aedon*). Larger-sized plastic bands could not be used to mark newly hatched nestlings because they tended to slide down over the nestling's toes and fall off completely. Stonehouse (1978) suggested using florist's wax to temporarily reduce the inside diameter of rings, but did not discuss the advantages or possible limitations.

Although nest disturbance may not have adversely affected growth or survival in this study, there are important consequences for researchers regarding marker application time and retention. Elastic bands applied to the tarsus had a high retention rate, but researchers who anticipate marking large numbers of nestlings should consider the time involved in applying the elastic bands. For instance, marking a brood of four nestlings would take approximately 10 min using elastic bands on the tarsi. Because some wetlands in our study area had 80 Red-winged Blackbird nests, approximately 800 min would have been required to mark all nestlings on that site. Investigators anticipating small sample sizes of marked nestlings, or inability to revisit the nest until

fledging, may consider the durability of this marking technique particularly advantageous.

Nestlings marked with either polish on the culmen, polish on the hallux, or ink on the tarsus never retained their marker for the duration of the nestling period. Strehl and White (1986) encountered similar problems (reapplication every 3rd day due to color loss) with Red-winged Blackbird nestlings marked under their wings with a colored, waterproof, felt-tip marker. These techniques should be considered only for nestling studies where it is possible to remark nestlings at least once every 4 days. Red-winged Blackbird nestlings that were remarked 4 days after hatching usually retained their marker for the remainder of the nestling period. Because these markers were among the quickest to apply, they would be especially suitable for nestling studies where large sample sizes are anticipated.

Although other marking techniques for nestlings may exist, our results demonstrate that superciliary down clipping is an inexpensive and safe technique to mark Red-winged Blackbird nestlings. Moreover, the entire marking process can be completed in seconds and the markings will be visible for the duration of nestling period.

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BREEDING BIOLOGY OF THE CHIPPING SPARROW IN PONDEROSA PINE FORESTS OF THE COLORADO FRONT RANGE

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ABSTRACT.—We present information on the breeding biology and nest-site characteristics of the western subspecies of the Chipping Sparrow (*Spizella passerina arizonae*) in montane ponderosa pine (*Pinus ponderosa*) forests of the Colorado Front Range. We located 83 nests during the summers of 1999–2002. The earliest egg date was 23 May and young fledged as late as 11 August. Nests were typically placed in needle clusters on outer branches of ponderosa pines. Mean canopy cover at nest sites was 50%. We observed no differences in nest placement or nest-site microhabitat between successful and unsuccessful nests. The nesting cycle lasted approximately 30 days, including 4 nest-building days, 3 egg-laying days, 14 incubation days, and 9 brooding days. Nests with known outcomes fledged a mean of 1.67 young from a mean clutch of 3.08 eggs. At least 27 nests (32.5%) were depredated, making predation the primary cause of nest failure. Of 42 successful nests, 5 (11.9%) were parasitized, although at least two Chipping Sparrows and one Brown-headed Cowbird (*Molothrus ater*) fledged from each parasitized nest. Both parasitism rates and nest success are highly variable among populations in this species. Received 16 October 2003, accepted 12 August 2004.

The Chipping Sparrow (*Spizella passerina*) is widespread throughout the United States and Canada. In Colorado, the western subspecies (*S. p. arizonae*) arrives in late April to early May and leaves in mid- to late September. In Colorado, it nests most commonly in ponderosa pine (*Pinus ponderosa*), riparian, pinyon-juniper (*Pinus edulis/Juniperus monosperma*), and Gambel oak (*Quercus gambelii*) woodlands, especially adjacent to meadows and canopy openings (Bailey and Niedrach 1965, Sedgwick 1987, Versaw 1998, Ortega and Ortega 2001).

Although the Chipping Sparrow is the most abundant species breeding in ponderosa pine habitats along the Front Range, its breeding biology, nest-site characteristics, and the effects of predation and Brown-headed Cowbird (*Molothrus ater*) parasitism are poorly understood because the nests are difficult to find (Middleton 1998, Ortega and Ortega 2001). Previous studies of Chipping Sparrows revealed that rates of nest loss due to predation range from 19.6 to 85% (Middleton 1998, Ortega and Ortega 2001).

Cowbird parasitism heavily impacts songbird nesting success in ponderosa pine forests of Colorado (Chace et al. 2003), especially

that of the Plumbeous Vireo (*Vireo plumbeus*) and Lesser Goldfinch (*Carduelis psaltria*) (Prather et al. 2002, Chace et al. 2003). Elsewhere, studies of Chipping Sparrow breeding biology have shown a wide range of parasitism. In Ontario, parasitism was 92% in one population but zero in another (Verner and Ritter 1983, Scott and Lemon 1996), and zero in California (Reynolds and Knapp 1984) and Louisiana populations (Goertz 1977).

During the summers of 1999–2002, we studied Chipping Sparrow breeding biology to determine the importance of predation, parasitism, and nest-site selection to overall nesting success in ponderosa pine habitats of north-central Colorado. Specifically, we located and monitored Chipping Sparrow nests to ascertain nest success, nest-site characteristics, and extent of parasitism by Brown-headed Cowbirds. We also conducted bird surveys to determine relative avian abundance during the breeding season.

METHODS

Study areas.—We located and monitored nests in open canopy ponderosa pine habitats near Boulder, Colorado, at two sites: (1) the City of Boulder Open Space and Mountain Parks and (2) Boulder County Open Space properties (40° 0' N, 105° 16' W). The vegetation is park-like, open canopy forest interspersed with grassy areas and denser stands of ponderosa pine. The main tree species is ponderosa pine with scattered Douglas-fir (*Pseu-*

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dotsuga menziesii). The understory contains various woody shrubs such as wax currant (*Ribes cereum*) and skunkbush sumac (*Rhus trilobata*) as well as various grasses (*Bromus* and *Stipa* spp.) and forbs (*Achillea* spp.).

Abundance.—We established 91, 50-m fixed-radius circular plots within the 2,500-ha study area. Each breeding season from 1999–2001, we visited all 91 points three times between 1 June and 15 July and counted birds according to methods detailed in Ralph et al. (1993). This method involves counting all birds seen or heard within a 50-m-radius circle during a 10-min census period. We then calculated relative abundance as mean number of pairs detected per point count census averaged across three counts per year. Other than Chipping Sparrows, the four most abundant species were Western Wood-Pewee (*Contopus sordidulus*), Spotted Towhee (*Pipilo maculatus*), American Robin (*Turdus migratorius*), and Western Tanager (*Piranga ludoviciana*). The detectability of these species was similar to that of Chipping Sparrows. In addition, in our study area habitats were very open, allowing a clear view of birds within 50 m, thus making varied detectability less likely. As a result, despite the limitations of this method, fixed-radius point counts accurately sampled the birds in the study habitat.

Nesting biology.—During the summers of 1999–2002, we monitored nests in accordance with protocol presented by Ralph et al. (1993). We monitored nests every 3 days, using either a 6-m telescoping mirror pole or by direct observation, until the nests were no longer active. Care was taken not to attract potential brood parasites or predators by approaching nests from random directions (Picozzi 1975, Major 1989). Nest searching began in May and concluded in August, when the last nests had fledged young. We recorded number of eggs laid, number of young hatched, nest attentiveness by parents, time of fledging, and nest fate. A nest was considered successful if it fledged at least one sparrow. We defined the incubation period as the time from the day the last egg was laid to the day the first egg hatched, and the nestling period as the time from the day the first egg hatched to the day the first young fledged. To calculate nesting success, we followed the methods proposed by Mayfield (1975), with adjustments sug-

gested by Manolis et al. (2000) for nests of unknown fates.

Microhabitat characteristics.—After nests were no longer active, we measured habitat characteristics at each nest site using standardized protocols (James and Shugart 1970, Martin and Roper 1988). Nest tree measurements included diameter at breast height (dbh), height of the nest and lowest living branch, distance from nest to trunk and tip of branch, canopy cover around the nest, nest orientation, and nest tree species. We measured heights of tall trees and higher nests with a Suunto PM-5/360 PC clinometer. We determined canopy cover by calculating the mean of four measurements taken with a Lemmon model-A convex spherical densiometer at a distance of 1 m from the nest in the four cardinal directions (Lemmon 1957).

We used *t*-tests (StatView, ver. 5.0.1; SAS Institute, Inc. 2002) to examine whether habitat variables were significantly related to nest outcome. Vegetation analyses were conducted for nests that had definitive outcomes ($n = 72$). Statistical significance was set at $P = 0.05$ and means are presented \pm SD.

RESULTS

Abundance.—The mean relative abundance of Chipping Sparrows was 1.03 ± 0.78 pairs/count ($n = 819$ point counts). Other common species included Western Wood-Pewee (0.96 pairs/count), Spotted Towhee (0.66 pairs/count), American Robin (0.49 pairs/count), and Western Tanager (0.41 pairs/count).

Nesting success.—We found a total of 83 nests (Table 1), with the earliest egg recorded on 23 May and the last nest fledging young on 11 August. Successful nests ($n = 42$) contained a mean of 3.00 ± 0.86 eggs and fledged 2.87 ± 0.96 young. For all nests across all 4 years, mean clutch size was 3.08 ± 0.86 ($n = 74$) and each nest fledged 1.67 ± 1.60 young (Table 1). In a nesting cycle of 30.3 days, mean nest-building, egg-laying, incubation, and nestling periods were 4.1, 3.2, 14.3, and 8.7 days, respectively.

Nine nests (10.8%) had unknown outcomes, 5 nests (6%) were abandoned, and 27 nests (32.5%) were depredated. Of the 42 successful nests, 5 were parasitized but still succeeded in fledging at least two Chipping Sparrows as well as one Brown-headed Cowbird each (Ta-

TABLE 1. Nest outcome, clutch size, and number of birds fledged from 83 Chipping Sparrow nests along the Colorado Front Range near Boulder, Colorado, during the summers of 1999–2002.

	1999	2000	2001	2002	All years
Total nests	24	22	19	18	83
Successful ^a	7	14	12	9	42 (50.6%)
Depredated ^b	12	7	4	4	27 (32.5%)
Abandoned	2	1	1	1	5 (6.0%)
Unknown	3	0	2	4	9 (10.8%)
Parasitized	0	1 ^c	4 ^d	1 ^c	6 (7.2%)
Mean clutch size	3.39 ± 0.72	2.67 ± 0.91	3.0 ± 0.77	3.50 ± 1.05	3.08 ± 0.86
Mean number fledged	1.04 ± 1.60	1.86 ± 1.64	1.56 ± 1.29	2.33 ± 1.87	1.67 ± 1.60

^a Includes five parasitized nests.

^b Includes one parasitized nest.

^c Fledged three sparrows and one Brown-headed Cowbird.

^d One parasitized nest was depredated, and three nests fledged two sparrows and one Brown-headed Cowbird each.

ble 1). All parasitized nests contained one cowbird egg.

Nesting success was 56.8% (following Mayfield 1975) and 31.6% (following adjustments suggested by Manolis et al. 2000). The probability of nest success was 0.713 in the egg-laying stage, 0.541 in the incubation stage, and 0.818 during the nestling phase. Daily rates of nest failure were 0.099, 0.043, and 0.023 during the egg-laying, incubation, and nestling phases, respectively.

Nest placement.—The most common nest tree was ponderosa pine (71.1%, $n = 59$), followed by common juniper (*Juniperus communis*; 13.3%, $n = 11$), Douglas-fir (8.4%, $n = 7$), and blue spruce (*Picea pungens*; 1.2%, $n = 1$). Two (2.4%) nests were in skunkbush, one (1.2%) was in wax currant, and the remaining two (2.4%) were in mountain mahogany (*Cercocarpus montanus*).

We collected detailed data on vegetation characteristics at 72 of the 83 nests. Sparrows tended to nest in clusters of pine needles on

outer branches with a mean distance of 1.36 m ± 1.45 between the nest and the trunk and a mean distance of 0.58 m ± 0.47 between the nest and tip of the branch. Nests were partially concealed with a mean canopy cover of 48.3% ± 23.9; the trees' lowest living branches were 1.19 m ± 1.43 above the ground. Most nests were constructed approximately one-third of the way up the tree; mean nest height = 2.55 m ± 2.50, and mean nest-tree height = 6.93 m ± 5.53 (Table 2). Orientation of the nest to the tree trunk was 155.7° ± 99.3 (Fig. 1). Orientation of nests was significantly clumped around the mean (Rayleigh test $r = 0.223$, $Z = 3.88$, $P = 0.021$). We found no significant differences between successful and unsuccessful nests for all measured microhabitat variables, including nest height ($t = 0.72$, $P = 0.24$), distance from nest to trunk ($t = 0.93$, $P = 0.18$), distance of nest from tip of branch ($t = 0.69$, $P = 0.25$), nest-tree height ($t = 0.04$, $P = 0.48$), lowest living branch of nest tree ($t = 1.39$, $P = 0.089$), dbh of nest

TABLE 2. Microhabitat characteristics (mean ± SD) of successful and unsuccessful Chipping Sparrow nests along the Colorado Front Range near Boulder, Colorado, 1999–2002. Microhabitat characteristics were not significantly different (all $P > 0.05$) between successful and unsuccessful nest sites.

Characteristic	<i>n</i>	Successful nests	Unsuccessful nests	Combined
Nest tree height (m)	72	7.22 ± 5.81	6.53 ± 5.20	6.93 ± 5.53
Nest height (m)	72	2.97 ± 2.92	1.96 ± 1.95	2.55 ± 2.50
Nest to trunk (m)	72	1.44 ± 1.50	1.23 ± 1.38	1.36 ± 1.45
Nest to tip (m)	72	0.62 ± 0.48	0.53 ± 0.45	0.58 ± 0.47
Lowest living branch (m)	70	1.36 ± 1.61	0.98 ± 1.13	1.19 ± 1.43
Diameter at breast height (m)	60	0.37 ± 0.16	0.31 ± 0.18	0.35 ± 0.17
Orientation (degrees)	70	176.23 ± 100.25	165.20 ± 88.66	171.50 ± 94.94
Canopy cover (%)	69	47.89 ± 24.67	48.86 ± 23.28	48.31 ± 23.91

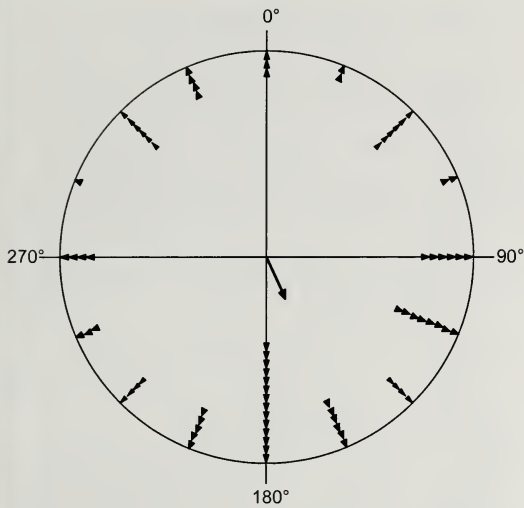


FIG. 1. Orientation of Chipping Sparrow nests relative to the trunks of nest trees along the Colorado Front Range near Boulder, Colorado, during the summers of 1999–2002. Mean orientation is represented by vector showing significant clumping of data (Rayleigh test $r = 0.223$, $Z = 3.88$, $P = 0.021$).

tree ($t = 0.89$, $P = 0.19$), canopy cover ($t = 0.07$, $P = 0.47$), or mean canopy height at nest site ($t = 0.83$, $P = 0.20$; Table 2).

DISCUSSION

On the Front Range, we found Chipping Sparrow nests with eggs as early as 23 May. Active nests were present through at least 11 August. Records of active nests from the Colorado Breeding Bird Atlas range from 17 May to 27 July (Versaw 1998). Ortega and Ortega (2001) reported that in southwestern Colorado clutches start as early as 14 May and nests are active as late as 19 July.

Chipping Sparrows mainly chose medium to large ponderosa pines and nested approximately one-third of the way up the tree and two-thirds of the way out on the branch. This finding is similar to that reported by Stull (1968), Andrews and Righter (1992), and Versaw (1998), but it contrasts to what was reported by Bailey and Niedrach (1965), who list shrubs as the most common nest substrate. Ortega and Ortega (2001) found that Chipping Sparrows in southwestern Colorado choose Gambel oaks, the most abundant shrub in that region. The preference shown for ponderosa pine in our study may reflect the tendency of

Chipping Sparrows to nest in the most commonly available substrate.

Nests were concealed in needle clusters and canopy cover was nearly 50%, typical of Chipping Sparrow nests (Middleton 1998). Stull (1968) and Reynolds and Knapton (1984) report that female Chipping Sparrows may use sunlight as a heat source while brooding, which may account for the significant south-southeast orientation of nests we found along the Front Range (Fig. 1).

Nest location and measured habitat variables were not significantly related to nest success, suggesting that predation pressure (the major cause of nest failure) may be similar across this forest type, regardless of microhabitat characteristics. Landscape context, as well as microhabitat features not measured in this study, such as tree density and nest concealment, may be important in determining success of nesting Chipping Sparrows.

We recorded a mean incubation period of 14.3 days, slightly longer than that reported by others (10.4 days, Ortega and Ortega 2001; 11–12 days, Reynolds and Knapton 1984). Middleton (1998) reports a range from other studies of 10–15 days. We found that the average duration from hatching until fledging was 8.7 days, similar to that found in previous studies (Reynolds and Knapton 1984, Middleton 1998, Ortega and Ortega 2001).

In southwestern Colorado, predation was the major cause of nest failure (85%; Ortega and Ortega 2001). In our study, predation also was the major cause of nest failure (84.8%). In Ontario and Minnesota, however, predation accounted for only 19.6% (Middleton 1998) and 55% (Keller 1979) of nest failures, suggesting that in Colorado predation may play a more prominent role in nest failure.

In southern Ontario, Graham (1988) found that 52% of Chipping Sparrow nests were parasitized, and Scott and Lemon (1996) reported a parasitism rate of 92%. However, no instances of parasitism were found in northern Ontario (Reynolds and Knapton 1984), nor were any found in Louisiana (Goertz 1977) or California (Verner and Ritter 1983). In southwestern Colorado, Ortega and Ortega (2001) suggest that Chipping Sparrows do not appear to be high-quality hosts compared with other hosts. They found that 17 of 77 nests (22%)

were parasitized and only 6% of all nests failed due to parasitism.

Despite being the most common species on our sites, from 1999–2002, Chipping Sparrow nests accounted for only 8.4% of the total 71 parasitized nests found (total nests with known outcomes = 450 for 10 species). In contrast, 50.7% of parasitized nests were those of Plumbeous Vireos, even though relative abundance of vireos was only 0.29 ± 0.42 pairs/ha. From 1984 to 2002, 146 (49.6%) vireo nests of known outcome were parasitized along the Front Range (Chace and Cruz 1996, 1999; Chace et al. 2000, 2003; J. F. Chace and A. Cruz unpubl. data), suggesting that the species is a preferred host in Colorado. Plumbeous Vireos may be more at risk from cowbird parasitism because they advertise the nest site by singing from the nest (Hahn et al. 1999). Additionally, although cowbirds have been characterized as host generalists, individual females may be host specialists. Alderson et al. (1999) found that half of the cowbird females at Delta Marsh, Manitoba, laid their eggs in the nests of a single host species, the Red-winged Blackbird (*Agelaius phoeniceus*). A potential preference for vireos and their unique susceptibility to parasitism—coupled with the fact that Chipping Sparrows elsewhere also often abandon parasitized nests—could account for lower parasitism of Chipping Sparrows along the Colorado Front Range.

The nesting biology of Chipping Sparrows in Colorado is similar to that reported in previous studies. Success and parasitism rates vary widely between study locations however. The broad range of habitats occupied by this species across North America may account for its plasticity in nesting biology.

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BLACK-CAPPED CHICKADEE DAWN CHORUS AND SUBSEQUENT SEXUAL ACTIVITY

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ABSTRACT.—Male Black-capped Chickadees (*Poecile atricapillus*) sing for several minutes prior to dawn during the breeding season. In northeastern Colorado, dawn singing was associated with male-female interactions rather than male-male interactions; males did not approach one another during the chorus. Males sang until female arrival, at which point they attempted copulation. During copulation attempts, males always uttered strings of *variable sees* and nearly always attached *gargles* to these strings. All *gargles* terminated in an acoustically similar, low-pitched, buzzy syllable. Received 30 January 2004, accepted 3 August 2004.

Several investigators have described behavior associated with copulation in Black-capped Chickadees (*Poecile atricapillus*; Dixon et al. 1970, Ficken et al. 1985, Smith 1991), but none mention preceding *fee-bee* singing behavior or the time-of-day during which copulation occurred. Other investigators have shown that attributes of the dawn chorus reliably reflect the social rank of males (Otter et al. 1997, Christie et al. 2004), and thus might be used by females to assess male quality. Otter and Ratcliffe (1993) found that the dawn singing bouts of male chickadees nearly always end with the arrival of a female and that copulation usually follows. They also found that experimental mate removal results in longer dawn bouts that continue until mates are returned. This paper confirms and expands on the studies mentioned above by reporting the behavior of several chickadee pairs following the dawn chorus and describing subsequent sexual interactions.

METHODS

I observed the dawn chorus of 17 mated, male Black-capped Chickadees between 04:00 and 05:30 MST at 14 study sites in northeastern Colorado in 2002 and 2003 (Table 1). Six study sites were in Fort Collins ($n = 9$ males), five sites were 14 to 28 km north of Fort Collins in isolated habitat patches containing ≤ 4 chickadee pairs per patch ($n = 1$ male/site), and the other three sites were in Loveland ($n = 1$ male), Fort Lupton ($n = 1$

male), and Sterling ($n = 1$ male). In each case, I observed one, unbanded male throughout his dawn singing bout and recorded his subsequent behavior. All males except one were observed during the typical breeding season (early April to mid-May); the remaining male was observed in mid-June (probably a second breeding effort). Two field assistants and I made field recordings of songs using a Sony minidisc recorder (either model MZ-R700 or model MZ-N1) connected to a Sennheiser microphone (ME62) mounted in a 60-cm Telinga Pro-universal parabola; we also narrated behavioral observations onto these recordings. When the focal male had stopped singing for at least 3 min, we assumed that his dawn singing bout had finished.

For each dawn singing bout, I recorded the following variables: whether a female arrived, the distance between where she was first detected and the location where the male began his singing bout, how many songs the focal male sang after her arrival, whether the male attempted copulation, and any male-male agonistic interactions during the bout. In all cases except one, the location of the female roosting cavity was unknown. A male-male agonistic interaction was defined as an approach by the focal male and a neighboring male to within 10 m of one another that led to displacement and/or *gargle* calls (Ficken et al. 1987) from either male. Males were within hearing distance of several other singing males during the dawn chorus, but I did not record whether males matched the songs of their neighbors. For all copulation attempts that immediately followed a dawn singing bout, I noted whether males used *variable see* and *gargle* calls (Ficken et al. 1985). It was

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TABLE 1. Summary of the behavior of 17 Black-capped Chickadee pairs during and after the dawn chorus, 2002–2003. Chickadees were observed in Fort Collins, Colorado (“FC,” $n = 9$ pairs), at five isolated study sites north of Fort Collins (“FCN,” $n = 1$ pair/site), and at three other study sites outside of Fort Collins ($n = 1$ pair/site). Asterisks indicate missing data. Females usually were first observed near where males began their dawn singing bouts. The exact female roost site was known only for the mate of “Ziggy.” Following the arrival of a female, a singing male usually ended his dawn bout and attempted to copulate with the female. Although female presence affected male behavior during the dawn chorus, singing males rarely approached other males.

Study site	Date	Breeding stage	Distance (m) ^a	Songs following female arrival	Copulation attempt following female arrival?	Male-male approaches during dawn bout
Loveland	7 Apr 2003	Pre-nest	10	0	Yes	0
FCN-StMa	10 Apr 2003	Pre-nest	50	0	Yes	0
FC-Dixon	15 Apr 2003	Nest-building	8	0	Yes	0
FC-ELC	16 Apr 2003	Pre-nest	20	0	Yes	0
FC-CSU	23 Apr 2002	*	15	0	Yes	0
FCN-Waver	25 Apr 2003	Egg-laying	10	0	Yes	0
FC-LMP	26 Apr 2002	*	*	0	Yes	1
FC-LMP	28 Apr 2003	Egg-laying	11	52	Yes	0
FC-LMP	28 Apr 2003	*	*	2	Yes	0
FCN-Ziggy	30 Apr 2003	Egg-laying	2	0	Yes	0
FCN-Ivan	3 May 2003	Nest-building	4	0	No	0
FCN-Zimd	5 May 2003	Nest-building	25	6	No	0
FC-ELC	6 May 2003	Incubation	18	9	No	0
FC-Cem	7 May 2003	*	*	3	Yes	0
Fort Lupton	15 May 2003	*	10	7	Yes	0
Sterling	16 May 2003	*	*	0	Yes	0
FC-Bed	18 Jun 2003	*	5	0	Yes	0

^a Distance between the observed location of the arriving female and the location where the male began his singing bout.

not always possible to monitor the vocal behavior of both the male and the female during copulation attempts, but when possible, I attempted to note whether the female used these calls as well. Because all birds were unbanded, I kept track of the observed male through constant visual monitoring during and after its dawn singing bout, and by observing any chases performed in a sexual context. (I never observed females chasing males in a sexual context.) I often observed wing-quivering in either or both males and females, but I did not consistently take data on this behavior so I do not report it. For 10 of the 17 pairs, I determined breeding stage by making additional observations for up to 2 hr after the end of the dawn singing bout. Breeding stage is important because pairs tend to cease sexual activity soon after beginning the incubation phase (Ficken et al. 1985).

RESULTS

Males always began singing prior to dawn and before any female activity; bouts never ended until female arrival. Eleven of 17 focal males stopped singing immediately after fe-

male arrival, and 5 sang fewer than 10 additional songs after female arrival (Table 1). The remaining male stopped singing temporarily after female arrival to copulate with her; he then continued singing in her presence for a few minutes before ending his overall dawn bout with another copulation attempt. In contrast to male-female interactions related to the dawn chorus, male-male interactions were rare. Only 1 of the 17 focal males was involved in a male-male agonistic interaction during his dawn singing bout (Table 1). This male displaced and chased a male unfamiliar to me that appeared on the focal male's territory 1 min prior to female arrival.

Females usually arrived near the location where the male chickadee began his dawn singing bout. For four of the males, I did not know exactly where the male chickadee began its dawn bout; for 12 of the remaining 13, the distance between the location where the male began singing and where the female was first detected was always ≤ 25 m (mean = 11.5 m ± 6.9 SD; Table 1). One male, whose mate's roosting location was known prior to observation, was particularly instructive. Although

he took several flights during his dawn bout, he spent approximately 75% of his time within 8 m of her roosting location and approximately 40% of his time within 2 m. While singing, he often approached and/or looked into the nest cavity.

For 14 of the 17 males, termination of the male's dawn singing bout was accompanied by a copulation attempt (Table 1). Only three males did not attempt copulation immediately after female arrival. Females of two of these males were in the nest-building phase, and copulation occurred >30 min after the dawn singing bout; interestingly, after both copulations, the females began gathering nesting material. The other female that did not copulate with her mate after her arrival was later confirmed to be in the incubation phase.

All 14 males that attempted copulation following their dawn bouts uttered strings of *variable see* calls during their copulation attempts, and 13 used combinations of *variable see/gargle* calls (Fig. 1A–D). During 9 of the 14 copulation attempts, females also vocalized, but none of these 9 females gave *variable sees* or *gargle* calls. The 13 males that gave *gargles* terminated their *gargles* with the same, low-pitched, buzzy syllable (Fig. 1A–D), although one male used an alternative syllable once before switching to several *gargles* containing the typical terminal syllable.

The terminal buzzy syllable of the *gargle* is apparently given in an agonistic context as well (see syllable 16 in Fig. 2 of Baker et al. 2000). In a laboratory setting, M. C. Baker recorded five males that he captured in Fort Collins in fall 2002 (males different from the 17 males discussed above). These five birds directed threat displays at their mirror-image reflections and gave *variable see/gargle* combinations that also contained the terminal buzzy syllable of the *gargle* (Fig. 1E–F; see Baker et al. 2000 for methods). Thus, it appears that regardless of context—whether agonistic or during copulation—combinations of Black-capped Chickadee *variable sees/gargles* may terminate with acoustically similar syllables.

DISCUSSION

From these data, several clear patterns emerged. Dawn singing by male Black-capped Chickadees during the breeding season was directed primarily at females rather than

at rival males, and females tended to arrive near the location where the male chickadee had begun singing his dawn bout. Males continued to sing until females arrived, at which time males attempted copulation. These patterns confirm earlier findings in Ontario (Otter and Ratcliffe 1993) and British Columbia (K. Otter pers. comm.); similar patterns have been found in Great Tits (*Parus major*; Mace 1986), Siberian Tits (*Parus cinctus*; Hailman et al. 1994) and Collared Flycatchers (*Ficedula albicollis*; Pärt 1991). Extra-pair copulations are common during the Black-capped Chickadee breeding season (Otter et al. 1998, Mennill et al. 2004). A comparison of the relative singing performances at dawn may provide females with a reliable indication of male quality (Otter et al. 1997, Christie et al. 2004), possibly explaining why Smith (1988) found that extra-pair copulations in chickadees nearly always occur within 1 hr of dawn.

Although males did not approach each other closer than 10 m, I cannot rule out the possibility that males used song during the dawn chorus to communicate with males as well as females. Male song might function simultaneously in both mate attraction and territorial defense (Mennill et al. 2002); however, the fact that males rarely approached each other during the dawn chorus, combined with the fact that males often approached each other later in the day in response to simultaneous male song (Shackleton and Ratcliffe 1994), suggests that song during the dawn chorus plays only a minimal role in male-male communication. Furthermore, Black-capped Chickadees in an Ontario population avoid matching the songs of neighboring males during the dawn chorus (Shackleton and Ratcliffe 1994), possibly because matching song in this population provokes a close approach by other males (Mennill and Ratcliffe 2004).

When attempting copulation, male chickadees always uttered strings of *variable sees* and nearly always followed these *sees* with *gargles*, similar to what was observed in previous studies of chickadee mating behavior (Dixon et al. 1970, Ficken et al. 1985). However, in contrast to previous studies (Dixon et al. 1970, Smith 1991), I observed no females giving *variable sees* or *gargles* during a copulation attempt. Smith (1991) mentioned that males might use a “special *gargle* call” as-

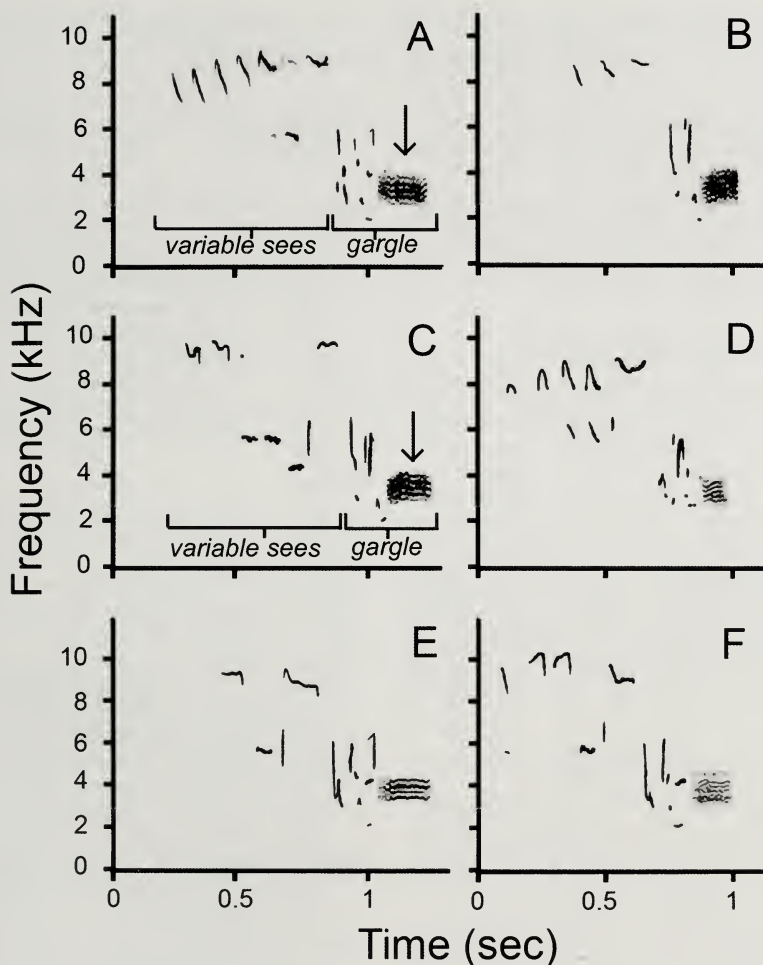


FIG. 1. Spectrograms showing Black-capped Chickadee *variable see* strings ending in *gargles* characterized by a special terminal syllable. All *variable see/gargle* combinations (components labeled in A and C) contained the same terminal syllable (arrow in A and C), regardless of whether they were used in male–female communication prior to a copulation attempt (calls A–D) or in male–male communication as part of an agonistic encounter (calls E–F). I made spectrograms using Syrinx software (<http://www.syrinxpc.com/index.html>) sampling at 22.05 kHz with 16-bit accuracy and 256-point FFT size (bandwidth = 43 Hz), and then transferring images to Adobe Photoshop 4.0 LE. Calls A, B, and C were obtained from males at three Fort Collins, Colorado, study sites in 2002–2003; call D was obtained from a bird at Fort Lupton, Colorado, 60 km from the Fort Collins study sites in 2003; calls E and F were also obtained from Fort Collins males, but these birds were captured in the field in fall 2002, and then their vocalizations were recorded in a laboratory setting by M. C. Baker using the methods described in Baker et al. (2000) (see text).

sociated with copulation, although she did not provide details on its acoustic structure. I found that *gargles* associated with copulation nearly always had a low-pitched, buzzy terminal syllable (Fig. 1A–D). This syllable appeared acoustically similar to the terminal syllables of copulatory *gargles* used by chickadees in Wisconsin (Ficken et al. 1985:fig. 1B), but not Tacoma, Washington (DEG pers.

obs.). *Gargles* used by Colorado chickadees in agonistic contexts possess a variety of terminal syllables, but *variable see/gargle* combinations used in agonistic contexts always terminated with the buzzy syllable, and the buzzy syllable is found in many *gargle* types not preceded by *variable sees* (Baker et al. 2000).

I speculate that the acoustic features of vo-

calizations associated with copulation (e.g., *variable sees* and the terminal buzzy *gargle* syllable) may affect female reproductive physiology, similar to the way in which a particular trilled syllable of a male Canary (*Serinus canaria*) affects female physiology (Vallet and Kreutzer 1995). This could be tested by playing male vocalizations to female chickadees and then monitoring their physiological and/or behavioral responses.

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AGGRESSIVE RESPONSES OF NESTING PRAIRIE FALCONS TO TERRITORIAL INTRUDERS

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ABSTRACT.—From 1984 through 1987, we studied aggressive responses of Prairie Falcons (*Falco mexicanus*) to species intruding into their nesting territories in southwestern Idaho (52 nesting attempts, 613 days, 9,085 hr). Prairie Falcons responded aggressively most frequently to Common Ravens (*Corvus corax*; 49% of encounters), followed by Red-tailed Hawks (*Buteo jamaicensis*; 24%), Golden Eagles (*Aquila chrysaetos*; 7%), Turkey Vultures (*Cathartes aura*; 4%), Northern Harriers (*Circus cyaneus*; 2%), American Kestrels (*Falco sparverius*; 1%), and bobcats (*Lynx rufus*; 1%). The frequency of aggressive responses toward intruders was similar for males and females, except in the case of American Kestrels and bobcats. Aggressive responses of nesting Prairie Falcons to intruders may be related to predator deterrence, competition for nest sites, stage of the nesting cycle, food availability, and sexual size dimorphism of falcons. Received 22 August 2003, accepted 16 August 2004.

Descriptions of aggressive responses of nesting Prairie Falcons (*Falco mexicanus*) are largely based on anecdotal information (e.g., Bent 1937, Enderson 1964, Ogden and Horrocker 1977, Anderson and Squires 1997) rather than systematic study. Nesting Prairie Falcons respond aggressively to a wide variety of avian and mammalian species that encroach into their territories, and they display varying levels of tolerance to intruding species (Steenhof 1998). The lack of systematically collected data has led to speculation about both the aggressiveness and tolerance of Prairie Falcons (e.g., Decker and Bowles 1930, Kaiser 1986). Here, we describe interspecific aggressive responses of Prairie Falcons to intruders in their nesting territories during the breeding season. We report on (1) species with which Prairie Falcons interacted, (2) the frequency of aggressive responses, (3) the level of aggression exhibited by Prairie Falcons, and (4) differences in aggressive responses between males and females.

METHODS

From 1984 through 1987, we observed Prairie Falcon pairs in 52 nesting attempts over 613 days (9,085 hr) in the Snake River Birds of Prey National Conservation Area (NCA; $n = 48$) and the Reynolds Creek Area ($n = 4$) in southwestern Idaho. The study ar-

reas are part of the western intermountain sagebrush steppe and are characterized by cold winters and hot, dry summers (West 1983). Climate, vegetation, and natural environment are described in U.S. Department of the Interior (1996). The data presented herein were collected as part of a larger behavioral study on Prairie Falcons (Holthuijzen 1989). General methodology, observation techniques, and protocol are described in Holthuijzen (1989, 1990). We defined nesting territory as a locality where nests were found, usually in successive years, and where no more than one pair ever nested at one time (Newton and Marquiss 1982). Between territory establishment and fledging of young, we observed each pair, on average, every 6 days. Observers were situated within 250 m of aeries (mean = 147 m \pm 43 SD, $n = 52$). An observation day started ½ hr before sunrise and terminated ½ hr after sunset. Field observations were made by two observers, each on a half-day shift. Observers were systematically rotated through all selected falcon pairs, alternating observations between mornings and afternoons. We began observations 1–7 weeks prior to incubation; observations continued until young were 30–35 days of age, or the nesting attempt failed. We used a photographic aging key (Moritsch 1983) to determine the age of young (when banded, visible at the aeries, or both). The beginning of incubation was calculated by back-dating from estimated age of young; we assumed that the incubation period was 34 days long (Burnham 1983). We pooled observation days into 6-day intervals.

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TABLE 1. Number of aggressive responses of male and female Prairie Falcons (52 nesting attempts, 613 observation days, 9,085 hr) directed toward territorial intruders in southwestern Idaho, 1984–1987.

Intruding species	Female			Male			Pooled observations			
	Chase	Vocal	<i>n</i>	Chase	Vocal	<i>n</i>	Chase	Vocal	<i>n</i>	%
Common Raven	328	224	552	364	160	524	692	384	1,076	49.5
Red-tailed Hawk	99	144	243	138	149	297	237	293	530	24.4
Golden Eagle	50	30	80	59	24	83	109	54	163	7.5
Turkey Vulture	16	32	48	23	15	38	39	47	86	4.0
Northern Harrier	21	7	28	19	3	22	40	10	50	2.3
American Kestrel	3	2	5	21	0	21	24	2	26	1.2
Bobcat	24	4	28	5	0	5	29	4	33	1.5
Other species ^a	13	12	25	9	5	14	22	17	39	1.8
Unidentified species	19	76	95	25	50	75	44	126	170	7.8
All species	573	531	1,104	663	406	1,069	1,236	937	2,173	

^a Osprey, Bald Eagle, Sharp-shinned Hawk, Northern Goshawk, Swainson's Hawk, Ferruginous Hawk, Rough-legged Hawk, gulls (*Larus* spp.), Barn Owl, Great Horned Owl, Black-billed Magpie, coyote, domestic dog, and porcupine.

The establishment of territorial boundaries early in the nesting season (Ogden and Horrocker 1977, Haak 1982, Sitter 1983, Holthuijzen 1989) and the general openness of the terrain enabled us to record aggressive responses between territorial falcon pairs and intruders in the nesting territories. We recorded time and duration of Prairie Falcon behaviors continuously, including aggressive responses to intruders that passed through nesting territories (Holthuijzen 1989). We defined an aggressive response as one during which the focal falcon engaged in aggressive behavior (multiple chases, vocalizations, or both) toward an intruder. We distinguished between two categories of aggressive responses: vocal (alarm call) and chase. We considered a chase, which often included vocalizing, a higher-intensity response than a vocal response alone. We defined a combined response as one in which both sexes of a nesting pair participated; falcon genders were determined by the larger size of females (Steenhof 1998), position during copulation, food solicitation by females, and stylized drawings of the facial patterns for each nesting pair. When an interaction took place, gender was either known at that time or was determined afterwards. Behavior of falcons was reported continuously during an observation day, minimizing gender misidentification.

We analyzed the number of aggressive interactions for male and female falcons separately, for each pair each day. We noted species of intruder and length of aggressive encounters. Statistical analyses were conducted

with Statistical Analysis System software (SAS Institute, Inc. 1990). Statistical tests were considered significant at $P \leq 0.05$. Differences in level of aggression between male and female Prairie Falcons were tested with Fisher's Exact Test. We calculated the number of interactions per hr during which paired birds were present on nesting territories and used one-way analysis of variance (ANOVA) to determine whether aggressive responses/pair/hr differed among nesting stages.

We did not collect information on relative abundance of intruders during the different phases of the Prairie Falcon nesting season. Therefore, our interpretations regarding temporal trends in aggressive responses to intruders by Prairie Falcons should be interpreted with caution.

RESULTS

Aggressive behavior of Prairie Falcons (both vocal and chase) was observed most often with Common Ravens (*Corvus corax*; 49% of encounters), followed by Red-tailed Hawks (*Buteo jamaicensis*; 24%), Golden Eagles (*Aquila chrysaetos*; 7%), Turkey Vultures (*Cathartes aura*; 4%), Northern Harriers (*Circus cyaneus*; 2%), American Kestrels (*Falco sparverius*; 1%), and bobcats (*Lynx rufus*; 1%) ($n = 2,173$ responses; Table 1). In 8% of all instances ($n = 170$), the intruder could not be identified. Fourteen additional avian and mammalian species intruded into falcon territories (2%, $n = 39$; Table 1): Osprey (*Pandion haliaetus*), Bald Eagle (*Haliaeetus leucocephalus*), Sharp-shinned Hawk (*Accipiter*

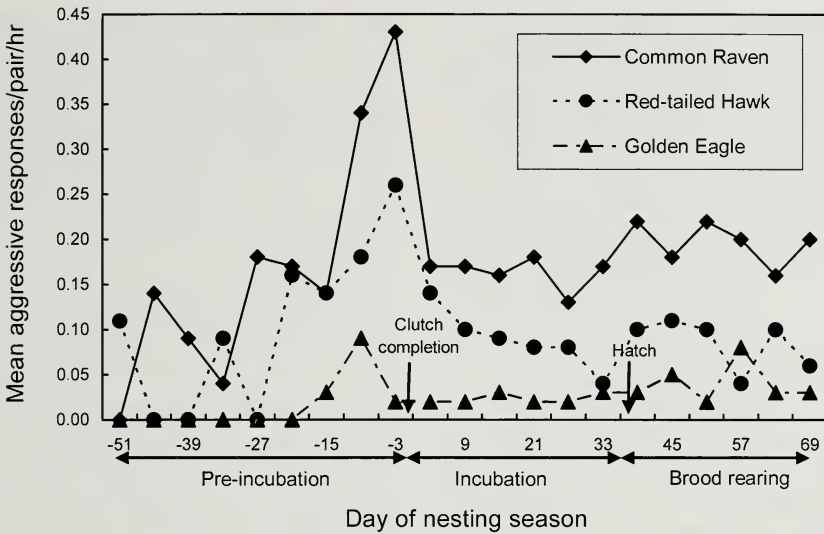


FIG. 1. Mean number of aggressive responses of Prairie Falcons on nesting territories (responses/falcon pair/hr; 52 nesting attempts, 613 days) directed toward Common Ravens, Red-tailed Hawks, and Golden Eagles in southwestern Idaho, 1984–1987.

striatus), Northern Goshawk (*Accipiter gentilis*), Swainson's Hawk (*Buteo swainsoni*), Ferruginous Hawk (*Buteo regalis*), Rough-legged Hawk (*Buteo lagopus*), gulls (*Larus* spp.), Barn Owl (*Tyto alba*), Great Horned Owl (*Bubo virginianus*), Black-billed Magpie (*Pica hudsonia*), coyote (*Canis latrans*), domestic dog (*Canis familiaris*), and porcupine (*Erethizon dorsatum*). Encounters averaged 1 min 56 sec \pm 2 min 35 sec (SD) and did not differ between male and female falcons (Student's *t*-test: $P = 0.25$).

The frequency of aggressive responses toward Common Ravens and Red-tailed Hawks was greater during pre-incubation than during incubation and brood rearing ($F_{2,594} = 5.79$, $P = 0.003$; $F_{2,594} = 7.37$, $P < 0.001$, respectively; Fig. 1), but did not differ between incubation and brood rearing for either species (Tukey's pairwise test, experimentwise error rates $P = 0.05$). Aggressive responses toward Golden Eagles were relatively stable over the breeding season ($F_{2,594} = 1.70$, $P = 0.18$; Fig. 1). Insufficient information was available to discern temporal patterns for other species.

The number of chases as a proportion of total aggressive responses was highest for American Kestrel (92%, $n = 26$), followed by bobcat (88%, $n = 33$), and Northern Harrier (80%, $n = 50$) (Table 1). We recorded 148

combined responses to intruders: Common Ravens made up 32%, Red-tailed Hawks 30%, Golden Eagles 16%, Northern Harriers 5%, and bobcats 3%.

Generally, the frequency of combined vocal and chase responses was similar for male and female falcons; the exceptions were American Kestrel and bobcat (Table 1). Males more frequently chased American Kestrels than females (Fisher's Exact Test: $P = 0.030$) and females chased bobcats more than males. Males more often chased Common Ravens than females (69%, $n = 524$ and 59%, $n = 552$, respectively; Table 1; Fisher's Exact Test: $P < 0.001$). Males chased Turkey Vultures more often (60%, $n = 38$), whereas females responded to them more often with vocalizations (67%, $n = 48$; Fisher's Exact Test: $P = 0.016$).

DISCUSSION

Prairie Falcons responded to avian intruders by vocalizing, chasing, or both; ground predators (i.e., bobcat and coyote) were mostly chased (Table 1). Aggressive responses of Prairie Falcons may reflect a perceived threat to nest or offspring. Prairie Falcons showed a relatively high percentage of combined responses toward Golden Eagles, Northern Harriers, bobcats, Red-tailed Hawks, American

Kestrels, and Common Ravens, but not to Turkey Vultures. Contrary to our findings, Kaiser (1986) reported that Northern Harriers and Turkey Vultures were largely ignored by nesting Prairie Falcons. Ogden and Hornocker (1977) and Kaiser (1986) reported that generally, Red-tailed Hawks and Golden Eagles are attacked (chased), as we found for Golden Eagles, but not for Red-tailed Hawks (Table 1). The vigorous response of Prairie Falcons to American Kestrels may be the result of provocation by kestrels, which tend to be very aggressive (Brown and Amadon 1968). Coyotes, bobcats (Ogden and Hornocker 1977, Sitter 1983, Kaiser 1986, Peterson 1988), and Golden Eagles (McFadzen and Marzluff 1996) are important predators of nestling and fledgling Prairie Falcons; thus, predator deterrence may be the predominant motivation for aggressive behavior of Prairie Falcons toward these species, particularly during brood rearing.

During pre-incubation, competition for nest sites may also play a role in high levels of aggressive responses of Prairie Falcons to Common Ravens and Red-tailed Hawks (Fig. 1). Alternatively, Red-tailed Hawks, Common Ravens, and Prairie Falcons establish nesting territories during approximately the same time, possibly increasing the frequency of encounters and raising opportunities for aggressive responses. Several authors (e.g., Bent 1937, Kaiser 1986, Anderson and Squires 1997) commented on the notable tolerance of Prairie Falcons for Common Ravens. Cade (1987) suggested a symbiotic relationship between Common Ravens and Prairie Falcons, whereby Prairie Falcons use nests built by Common Ravens and Common Ravens benefit by robbing prey cached by Prairie Falcons.

Food competition may explain some of the aggressive responses observed. Northern Harriers (Holthuijzen et al. 1987) and Red-tailed Hawks (Haak 1982) have been observed to kleptoparasitize adult falcons. Furthermore, scavengers such as Common Ravens and, perhaps, Turkey Vultures, may rob prey caches (Bent 1937, Cade 1987).

Female Prairie Falcons are about one-third larger than males (Enderson 1964), which may result in a differential response toward potential predators, as has been suggested for

other diurnal raptors (Newton 1979). Female falcons were responsible for 85% of the encounters with bobcats, and both males and females responded with high intensity to this species (100% and 86% chase, respectively; Table 1). The larger size of females may be a more effective deterrent against bobcats than the greater agility of males. On the other hand, American Kestrels were always chased by male Prairie Falcons; in this case, the agility of the male may be more effective. Toward other intruders, however, male and female Prairie Falcons showed a similarly aggressive response (Table 1). Apparently, size, agility, or other factors related to the size difference between males and females do not provide either gender with a particular advantage in defense against these intruders.

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THE NEST, EGGS, AND NESTLINGS OF THE CASTELNAU'S ANTSHRIKE (*THAMNOPHILUS CRYPTOLEUCUS*), WITH NOTES ON ITS ECOLOGY AND CONSERVATION

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ABSTRACT.—I present the first description of the nest, eggs, and nestlings of the Castelnau's Antshrike (*Thamnophilus cryptoleucus*). During June and July of 2003, I observed three nests of *T. cryptoleucus* in riverine habitats along the Río Amazonas, downstream from Iquitos, Departamento Loreto, Perú. The nests were deep, thin-walled cups suspended from the surrounding vegetation 1–3 m above the ground. The clutch size was two, and the eggs were cream-colored with reddish-brown markings. I found two nests on islands in the Río Amazonas and one nest on the mainland, providing evidence that *T. cryptoleucus* is not exclusively restricted to river islands. Two nests were in river-edge forest dominated by *Cecropia*, and one was in second-growth scrub next to a banana plantation, suggesting some tolerance of anthropogenic disturbance. All three nests were active during the period when the annual floodwaters were receding. Nest placement, structure of the nest, clutch size, and appearance of the eggs were all similar to those of the closely related Blackish-gray Antshrike (*Thamnophilus nigrocinereus*) and are typical of the genus. Received 24 March 2004, accepted 29 July 2004.

Castelnau's Antshrike (*Thamnophilus cryptoleucus*) occurs in western Amazonia (western Brazil, northeastern Perú, southeastern Colombia, and northeastern Ecuador), where it is locally fairly common in riverine forests, particularly on river islands (Sibley and Monroe 1990, Ridgely and Tudor 1994, Stotz et al. 1996, Zimmer and Isler 2003). The natural history and ecology of *T. cryptoleucus* are poorly known (but see Rosenberg 1990), and there is no previously published description of its nest, eggs, or nestlings (Zimmer and Isler 2003). While conducting fieldwork during the summer of 2003 on islands in the Río Amazonas downstream of Iquitos in Departamento Loreto, Perú, I found three nests of *T. cryptoleucus*, one of which I monitored periodically over 16 days.

Description of nest and eggs.—I found the first nest on 13 June in river-edge forest on the south bank of the Río Amazonas near the mouth of the Quebrada Yanayacu (3° 33' 35" S, 73° 03' 28" W). The second nest was found on 11 July near the edge of a cultivated banana grove adjacent to second-growth scrub on Isla Padre in the Río Amazonas near Iquitos (approximately 3° 38' S, 73° 06' W; exact coordinates not taken). I found the third nest on 14 July in river-edge forest on an unnamed island in the Río Amazonas near the mouth of

the Quebrada Yanamono (3° 27' 51" S, 72° 48' 25" W).

The first nest was located in a patch of young river-edge forest characterized by a low (approximately 6 m in height) canopy dominated by *Inga* trees, with some taller, emergent *Cecropia* trees. The shrub layer was dominated by *Heliconia*. The nest was approximately 20 m from the water's edge and an equal distance from a small (0.5–1 ha) clearing planted in yuca (*Manihot*), bananas, corn, and other crops. I conducted a detailed analysis of the vegetative structure of the river-edge forest at the site of the first nest. I recorded ground cover (80% forbs, 20% leaf litter), number of stems <2.5 cm in diameter (368), number of stems 2.5–8.0 cm in diameter (17), canopy density (95% closed), and canopy height (5.9 m) within a 5-m-radius sampling plot centered on the nest. I also recorded diameter at breast height of all stems >8 cm in diameter within an 11.3-m-radius tree sampling plot centered on the nest (*Inga*: 13.8 cm ± 2.9 SD, $n = 6$; *Cecropia*: 16 cm, $n = 1$; snag: 9 cm, $n = 1$). I found the second nest in a densely populated section of river-front, where the habitat consisted of interspersed home sites, agricultural clearings, and patches of natural second-growth vegetation. The nest was located near the edge of a clearing planted in bananas and a patch of scrubby second-growth vegetation. The nest was >100 m from the water's edge. The third nest was located in a patch of river-edge forest char-

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acterized by a relatively open canopy of *Cecropia* trees 20 m in height and a dense understory of *Gynerium* cane. The nest was approximately 30 m from the water's edge, and there were no clearings on the island where the nest was located.

All three nests were suspended by the rim from live vegetation. The first nest was 0.8 m above the ground in a 4-m-high shrub, the central stem of which was 5 mm in diameter at 1 m above the ground. The nest was suspended in a horizontal fork 0.3 m from the central stem. It was attached to two branches, which were 5 mm and 4 mm in diameter. The nest was approximately 80% concealed by leaves from above. Side concealment from different angles ranged from less than 10% to nearly 90%. The second nest was placed approximately 1.25 m above the ground in a sapling that was approximately 1.5 m in height. It was suspended between two branches of a horizontal fork, and was poorly concealed by the surrounding vegetation. The third nest was much higher, nearly 3 m above the ground. The nest was attached at the rim to three small vines, all of which were <10 mm in diameter. The vines supporting the nest hung down from a much thicker tangle of vines, so that the nest was fairly exposed from the sides, but almost entirely concealed from above by the bulk of the vine tangle.

The nest of *T. cryptoleucus* is fairly typical of those of other members of the genus *Thamnophilus*. The first nest was a deep, thin-walled cup attached by the rim in a horizontal fork (Fig. 1). It was composed primarily of grass, with some seed heads and small vines included. There was no distinct nest lining and no decoration on the outside of the nest. The nest was deeper than it was wide, and had very thin walls. The outer diameters were 80 and 120 mm, and the outer height was 145 mm. The inner diameters were 50 and 70 mm, and the inner depth was 105 mm. The second and third nests were similar in construction to the first. The second nest was also similar in size to the first, but the third nest was slightly smaller (exact measurements not taken).

The eggs and clutch size of *T. cryptoleucus* are also typical of the genus. The first and second nests each contained two eggs when discovered (the third contained two nestlings). The oval-shaped eggs were cream-colored

with a dense scattering of irregular, reddish-brown markings distributed evenly across the surface. The two eggs from the second nest measured 26 × 18 mm and 25 × 18 mm.

The first nest was visited periodically over 16 days during the late incubation and early nestling stages. On 13 June, and again on 16 June, an adult female was flushed from the nest, which contained two eggs. On 20 June, the nest was unattended and contained two gray-skinned nestlings, which were unfeathered and had not opened their eyes. On 22 June, and again on 26 June, the male and female adults scolded from nearby as I checked the nest, which still contained the two nestlings. By 26 June, approximately 8 days after hatching, the nestlings had pin feathers but no down feathers. On 29 June, 10 to 12 days after hatching, the nestlings were gone. The second nest was visited only once. An adult female was flushed from the nest, which contained two eggs. The third nest was visited only twice, on 14 June and 16 June. During both visits, the nest contained two nestlings and was unattended by an adult.

I was unable to determine the fate of the first nest with certainty. Antbirds often have relatively short nestling periods for their body size (Skutch 1976), varying from 8 to 16 days (Skutch 1996, Zimmer and Isler 2003). Therefore, it is possible that the nestlings from the first nest did fledge (10–12 days after hatching), although the presence of (only) pin feathers at approximately 8 days after hatching suggests a longer nestling period in *T. cryptoleucus*. Also, the nest was partially torn from its supporting branches, which suggests that the nest may have been depredated. Ultimately, I was unable to accurately determine the length of the incubation or nestling periods, but the development of the nestlings in the first nest was typical of that described for other antbirds (Skutch 1996).

Timing of breeding.—The annual flood peak at Iquitos, Perú, occurs during May, at which time most of the islands and the mainland immediately adjacent to the river are inundated; the flood recedes rapidly during June and July, reaching an annual low during August or September (Bodmer 1990). The three nests of *T. cryptoleucus* that I found were all active during the period when the floodwaters were receding. The eggs in the first nest



FIG. 1. Nest of Castelnau's Antshrike (*Thamnophilus cryptoleucus*), found in a shrub in river-edge forest on the south bank of the Río Amazonas, downstream from Iquitos, Departamento Loreto, Perú, June 2003. Illustration by JWA.

hatched on or around 18 June; thus, presumably they were laid around 4 June. If correct, construction of the nest would have begun in late May, just as the floodwaters began to recede. Because the nest was located on a natural levee along the river, the ground under the nest probably would not have been inundated, even at the peak of the flood pulse, though much of the surrounding river-edge forest would have been inundated.

Collections at the Louisiana State University Museum of Natural Science (LSUMNS) and the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos contain specimens of male and female *T. cryptoleucus*—in breeding condition—that were

collected from unflooded islands in the Río Amazonas in Perú during the months of July and August. The LSUMNS collection also contains a male specimen in breeding condition that was collected on the Río Santiago in Perú during the month of October. Finally, Russell and Lamm (1978) collected a pair in breeding condition on a partially flooded island in the Río Amazonas in Colombia during the month of March. No specimens or observations are available from other months of the year, so the length of the breeding season of *T. cryptoleucus* cannot be determined.

Comparison with other Thamnophilids.—Twenty-six species are currently recognized within the genus *Thamnophilus*, and the nest

and eggs have been described for 15 of these (Zimmer and Isler 2003). The nest structure, placement of the nest, clutch size, and the appearance of the eggs are similar among all species for which the nest and eggs have been described (Zimmer and Isler 2003). *T. cryptoleucus* was originally described as a subspecies of the Blackish-gray Antshrike (*T. nigrocinereus*) but has subsequently been elevated to species rank and is considered to form a superspecies with *T. nigrocinereus* (Hilty and Brown 1986, Sibley and Monroe 1990, Zimmer and Isler 2003). The nest and eggs of *T. cryptoleucus* are similar to those of *T. nigrocinereus* and are typical of the genus.

The typical *Thamnophilus* nest is a deep cup of woven grasses suspended by the rim in the fork of a branch, usually within 4 m of the ground (Zimmer and Isler 2003). The nest of *T. nigrocinereus* is a deep cup of woven plant fibers and spider silk suspended from the rim in a horizontal fork of a small bush 1–2 m above the ground (Zimmer and Isler 2003). The nest of *T. cryptoleucus* is similar to that of *T. nigrocinereus*, but none of the three nests of *T. cryptoleucus* that I observed included conspicuous spider silk. The clutch size is typically two in the genus *Thamnophilus* (Zimmer and Isler 2003); the clutch size of *T. nigrocinereus* is two (Zimmer and Isler 2003), as is that of *T. cryptoleucus*. *Thamnophilus* eggs are generally white, cream-colored, or pinkish and spotted or otherwise marked with brown, reddish-brown, or purplish colors. The markings are often concentrated in a wreath at the larger end of the egg, but may be evenly distributed across the egg (Zimmer and Isler 2003). The eggs of *T. nigrocinereus* are creamy white with large, violet-brown spots that are denser at the larger end of the egg (Zimmer and Isler 2003). The eggs of *T. cryptoleucus* are also creamy white, but with reddish-brown markings that are more or less evenly distributed across the surface of the egg.

Ecology and conservation.—*T. cryptoleucus* is often considered a river-island obligate (Hilty and Brown 1986, Sibley and Monroe 1990, Ridgely and Tudor 1994, Ridgely and Greenfield 2001), although it sometimes occurs on the mainland in successional habitats (Stotz et al. 1996, Zimmer and Isler 2003; JWA unpubl. data). J. P. O'Neill (pers. comm.)

observed a resident pair in river-edge forest on the mainland along the Río Santiago in Perú. I have found *T. cryptoleucus* in river-edge forest and in anthropogenically disturbed habitats at both island and mainland sites along the Río Amazonas, downstream of Iquitos, Perú. The presence of an active nest of *T. cryptoleucus* in river-edge forest on the mainland provides further evidence that the species is not always an island obligate and that resident breeding populations occur on the mainland.

The presence of an active nest at the edge of an actively managed banana grove suggests that *T. cryptoleucus* is fairly tolerant of human disturbance. In fact, anthropogenic disturbance may play an important role in maintaining appropriate habitat on the mainland for *T. cryptoleucus* and other avian species that have often been considered river-island obligates, but which occur on the mainland at the sites I have studied. Although *T. cryptoleucus* is not currently considered to be threatened (Stotz et al. 1996, Zimmer and Isler 2003), the total population size is probably small (Rosenberg 1990, Zimmer and Isler 2003), and the species would be vulnerable to anthropogenic changes in the hydrological regime within Amazonia (Remsen and Parker 1983, Rosenberg 1990, Zimmer and Isler 2003) due to dam construction (Borges and Carvalhaes 2000), deforestation (Gentry and Lopez-Parodi 1980), or global climate change (Nijssen et al. 2001). Because rivers are important transportation corridors throughout much of Amazonia, lands adjacent to the rivers are often the first to be developed; in addition, few floodplain areas in Amazonia are protected as parks or reserves (Borges and Carvalhaes 2000, Parra et al. 2001). Consequently, many riverine species are threatened by direct conversion of their habitat for agriculture. The ability of *T. cryptoleucus* to adapt to anthropogenic habitats would significantly mitigate the impact of anthropogenic habitat alteration.

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Short Communications

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When Should Mayfield Model Data be Discarded?

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ABSTRACT.—Much confusion exists over the proper way to handle nest-fate data collected after the fledge date when using the Mayfield method. I provide a simple numerical example showing how use of these data can bias estimates of daily survival probability, and present a likelihood function demonstrating that nest-fate data collected after the fledge date do not contribute any information for parameter estimation, except in a seldom-realized special case. Consequently, it is recommended that under the Mayfield model, nest-fate data collected after the fledge date be discarded. *Received 16 April 2004, accepted 31 July 2004.*

Previously, I presented a generalization of the Mayfield method (Mayfield 1961, 1975) for estimating daily survival probabilities of nests, and advocated discarding nest-fate data collected after the fledge date of a nest (Stanley 2004). The reason for this recommendation is that errors or uncertainty in determining nest fate after the fledge date, combined with decisions by the investigator as to how these data should be handled, can unnecessarily bias estimates of daily survival probability. Because this problem also manifests itself in the widely used Mayfield model for daily survival probabilities, and because (in my experience) there continues to be confusion regarding when and why such data should be discarded (Manolis et al. 2000), I present in this note a simple numerical example illustrating the problem and how it can be avoided. My goal is to bring clarity to, and increase awareness of, this issue.

Let us suppose we have a population of 32 nests, each containing exactly one nestling, and that the daily survival probability (p) for those nests is 0.5 (these numbers were chosen for illustrative purposes, and are not intended to be realistic). Further, suppose that we know every nest is exactly 2 days from fledging, and that after the first day 16 nests survive and 16

fail, and after the second day 8 of the 16 remaining nests survive to fledging and 8 fail before fledging. Finally, of the eight nests that failed during the second day, assume that at four of the nests there was obvious evidence that the nest had been depredated (e.g., feathers, tissue remains), and at the remaining four nests there was no evidence (e.g., the nestling was carried off). If we were studying this population of nests and had perfect knowledge of the situation just outlined (except for p), then the likelihood function (L) under which we would estimate p would be proportional to $p^{16}(1-p)^{16}p^8(1-p)^8$ (Johnson 1979), and our maximum likelihood estimate of p would be $\hat{p} = (16 + 8)/(32 + 16) = 0.5$. This estimate is mathematically equivalent to the usual Mayfield estimate, and is unbiased.

Now consider a slightly different situation, where we have the same information as above except that we do not know the fate of every nest after the second day because when we arrived at nests they were empty. We are, however, able to correctly deduce that at least 4 of the 16 nests failed because there were feather and tissue remains and we knew the nests contained only one nestling. How should we analyze these data? I present three scenarios:

Scenario 1.—Because we found no evidence to the contrary, and because the nestlings were gone from the nest, we assume the 12 nests without evidence of predation successfully fledged young. Under this assumption we get $L \propto p^{16}(1-p)^{16}p^{12}(1-p)^4$, and $\hat{p} = (16 + 12)/(32 + 16) = 0.583$. This estimate is positively biased, because the true $p = 0.5$.

Scenario 2.—Because we only know with certainty that four nests failed after the second day, we only use those data in our analysis. This is equivalent to assuming there were only 4 nests at risk of predation the second day (instead of 16); therefore, $L \propto p^{16}(1-p)^{16}p^0(1-p)^4$, and $\hat{p} = (16 + 0)/(32 + 4) = 0.444$. This estimate is negatively biased.

Scenario 3.—Because we cannot determine

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unequivocally the fate of *every* nest checked after the second day (the fledge date), we discard all data for nests checked after the fledge date. Under this scenario we get $L \propto p^{16}(1-p)^{16}$, and $\hat{p} = (16)/(32) = 0.5$. This estimate is unbiased.

Of the three scenarios presented, only the last yields an unbiased estimate of p . We were able to use data collected after the first day because we knew the nests were 2 days from fledging when they were found; hence, we knew the 16 empty nests found after the first day had to have failed. However, when we found 16 empty nests after the second day we could not be certain of the fate of every nest (only 4 of them). Consequently, it was necessary to discard all data from the second day so we would not bias our estimate.

The situation above, where knowledge of nest fate is imperfect, was simplified to illustrate the main point of this note. In reality, there are likely to be some nests checked after fledging where failure or success can be determined without error. If we let r_1 be the probability a nest checked after the fledge date is determined to have succeeded when it did, in fact, succeed, and let r_2 be the probability a nest checked after the fledge date is determined to have failed when it did, in fact, fail, then the appropriate model for our data (continuing with the example above) is

$$L \propto p^{n_1}(1-p)^{n_2}(r_1p)^{n_3}[r_2(1-p)]^{n_4} \\ \times [(1-r_1)p + (1-r_2)(1-p)]^{n_5}.$$

Here, n_1 and n_2 are the number of nests surviving or failing after the first day, n_3 and n_4 are the number of nests known with complete certainty to have survived or failed over the second day (i.e., known-fate nests checked after the fledge date), and n_5 is the number of nests checked after the fledge date where fate could not be determined with complete certainty (in the preceding numerical example $n_1 = 16$, $n_2 = 16$, $n_3 = 0$, $n_4 = 4$, and $n_5 = 12$). Using standard maximum likelihood methods under the assumption that $r_1 \neq r_2$, it can be shown that the maximum likelihood estimate for p is $\hat{p} = n_1/(n_1 + n_2)$. In other words, none of the nest-fate data collected for nests after the fledge date (i.e., n_3 , n_4 , or n_5) contributes information to the parameter estimate, even though the fate of some of those nests is

known with certainty. It is as if the data did not exist, or were discarded. Only in the special case where $r_1 = r_2$ (and $r_1, r_2 > 0$) do nest-fate data collected after the fledge date contribute to the estimate of p . In that case, $\hat{p} = (n_1 + n_3)/(n_1 + n_2 + n_3 + n_4)$. Because in real-world situations it will almost always be the case that $r_1 \neq r_2$, and because r_1 and r_2 will usually be unknown (so equality can not be ascertained), it is evident that nest-fate data collected after the fledge date should almost always be omitted from analyses under the Mayfield model (i.e., scenario 3 above). Attempts to use these data in an *ad hoc* fashion, as was illustrated by scenarios 1 and 2 above, will only serve to bias what would otherwise be an unbiased estimate.

In the material above, I have shown that even under ideal conditions—where nests are checked daily, the exact fledge date is known, and there is only one nestling per nest—nest-fate data collected after the fledge date do not contribute information for parameter estimation under the Mayfield model, and, if used in an *ad hoc* fashion, will introduce bias. In reality, the situation is even worse than I have portrayed. In most studies, nests are not checked daily and the exact fledge date is unknown. Consequently, evidence that might indicate nest fate (e.g., the presence of nearby young, tissue remains) will have had time to disappear, and we do not know how many days passed before the nest failed or fledged. Thus, we do not know the number of “nest days” to credit to a nest and this can create additional bias, even in the special case where $r_1 = r_2$. Furthermore, for many species there is often more than one nestling present and this will further complicate accurate assignment of nest fate. For example, suppose a nest contained three nestlings and that two fledged before the third nestling was taken by a predator. We would likely conclude the nest had failed, even though it actually succeeded. Once again, this can create additional bias. These real-world complications only serve to reinforce the main message of this paper, that nest-fate data collected after the fledge date—or more precisely, the predicted fledge date as determined by the investigator—should be omitted from the analysis.

The Mayfield model was developed under the assumption that daily survival probability

(p) is constant, when, in reality, p is probably heterogeneous (Stanley 2000, Dinsmore et al. 2002, Stanley 2004). If p is heterogeneous, and if the interval between nest checks is long, then it is possible that discarding nest-fate data collected after the fledge date will result in a loss of information about the nature of heterogeneity in p near the fledge date, and this could adversely affect robustness of the Mayfield estimator (D. H. Johnson pers. comm.). To prevent the loss of such information, investigators should make every effort to check nests more frequently as the predicted fledge date approaches. Not only will this lead to more robust estimates under the Mayfield model by decreasing the net information loss from discarded data, but it also will allow investigators to continually update the predicted fledge date so that in the end it more closely approximates the actual fledge date, thereby improving estimates.

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Predation of a Golden-cheeked Warbler Nest by a Western Scrub-Jay

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ABSTRACT.—I observed a Western Scrub-Jay (*Aphelocoma californica*) consume a Golden-cheeked Warbler (*Dendroica chrysoparia*) nestling and a Brown-headed Cowbird (*Molothrus ater*) nestling in northwestern Travis County, Texas, in May 1995. During a 4.5-hr period after brood destruction, warbler adults repeatedly brought insects to the depredated nest, and during each visit they appeared to search for the nestlings in the nest area and adjacent trees while carrying the insects. When the jay subsequently returned to the nest to take an unhatched egg, the female warbler performed a distraction display. My observations indicate that, in some cases, parental feeding behavior and nest defense can continue for a short time after brood loss. *Received 27 March 2002, accepted 28 May 2004.*

The Golden-cheeked Warbler (*Dendroica chrysoparia*) is an endangered species that breeds only in mature oak (*Quercus* spp.)-Ashe juniper (*Juniperus ashei*) forests or woodlands in central Texas. Nest predation is an important cause of mortality for this species (Gass 1996, Jette et al. 1998, Ladd and Gass 1999) and has been described in detail only for rat snake (*Elaphe guttata*) predation (Pulich 1976, Stake 2001) and Brown-headed Cowbird (*Molothrus ater*) predation (Stake and Cavanagh 2001). Documentation of parental behavior in response to predation is especially scarce. Here, I provide the first detailed account of nest predation at a Golden-cheeked Warbler nest by a Western Scrub-Jay (*Aphelocoma californica*) and describe warbler behavior in response to predation.

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I recorded this observation during a study of Golden-cheeked Warblers at the Balcones Canyonlands National Wildlife Refuge in northwestern Travis County, Texas (30° 30' N, 97° 58' W). The warbler nest was 3.2 m high in a 4.5-m high Ashe juniper on the south-facing slope of a sparsely wooded canyon. It contained one 3- to 4-day old Golden-cheeked Warbler nestling, one 4- to 5-day old Brown-headed Cowbird nestling, and one unhatched Golden-cheeked Warbler egg (L. Gass pers. comm.). I watched the nest for a total of 5 hr and 24 min from a distance of 10 m using a spotting scope and 8 × 42 binoculars.

On 16 May 1995 at 07:40 CST, an adult Western Scrub-Jay began foraging on the ground near the warbler nest, during warbler feeding visits. When it was 8 m from the nest tree, the jay stopped foraging and flew to a branch below the nest. After hopping from branch to branch for several seconds, the jay flew to the limb supporting the nest, and the nestlings began vocalizing with typical begging calls. The jay grasped the cowbird nestling by the neck and carried it to the ground. The jay vigorously pecked at the nestling several times and tore off and swallowed several chunks of flesh. My view was partially obscured, but I presume that the jay consumed the entire nestling, as no prey remains were later found at this location. Immediately afterwards, the jay returned to the nest, removed the warbler nestling, carried it to the ground, and consumed it in the same manner. The jay then returned to the nest a third time, picked up the remaining warbler egg, placed it back in the nest, and flew off. This series of events lasted about 2 min, during which the adult warblers were apparently unaware of the jay's presence. Five min later, the female warbler brought an insect to the nest, swallowed it immediately upon perching over the nest, consumed a fecal sac, and departed. The warbler did not appear to be alarmed during this visit. During the next 4 hr and 22 min, the adults brought insects to the nest seven times. They perched at the nest with food in their bills, uttered repeated "chip" notes (Pulich 1976), and swiftly hopped around the nest, nest branch, nest tree, and neighboring trees. I interpreted these behaviors as searching bouts, where the adults were apparently in search of their nestlings. Each bout lasted approximate-

ly 5–30 sec, totaling about 90 sec for the female and 40 sec for the male over the entire observation period. After each of these bouts, the warblers returned to the nest and either swallowed the insect they were carrying, or departed from the nest area with the food still in their bills. During three visits, the parents spent several seconds probing for and consuming fecal material from the bottom of the nest.

At 12:45, I again observed a Western Scrub-Jay (presumably the same individual) foraging on the ground near the nest. The warblers began chipping excitedly in the trees above the jay, and at 12:48, when the jay was foraging 15 m from the nest tree, the female performed a distraction display 3–4 m from the jay. With its tail feathers spread and wings fluttering, the warbler chipped rapidly and hopped gradually along a low branch. The jay did not appear to react to this display, and it continued foraging. At 12:50, the jay, 10 m from the nest tree, flew directly to the warbler nest and carried the remaining egg to a nearby branch. While the jay held the egg against the branch with its feet and began to consume the egg, the adult warblers chipped loudly close by. The jay did not appear to react to the warblers and several seconds later flew from the nest area. The warblers remained in the nest area and chipped loudly for 11 min, but no additional parental feeding bouts were observed. I stopped watching the nest at 13:15.

Whereas Western Scrub-Jays were considered likely nest predators of Golden-cheeked Warblers before this observation was recorded (U.S. Fish and Wildlife Service 1990), this is the first detailed description of Golden-cheeked Warbler nest predation by this species. (A summary of this observation is cited in Ladd and Gass 1999 as "J. Petick [sic] pers. comm.") Reported responses of adult Golden-cheeked Warblers to predators have included injury feigning displays, wing fluttering, agitated calling, flying away into the tree canopy, and remaining still or silent for prolonged periods (Ladd and Gass 1999: JP pers. obs.). The warblers' behavior during this predation event is noteworthy because of the repeated delivery of food to the depredated nest, the apparent bouts in search of young, and the distraction display following predation. These observations indicate that, in some cases, parental feeding behavior and nest de-

fense can continue for a short time after brood loss.

I offer two possible explanations for the warblers' response to nest predation. First, the warblers' reaction may have been due to a strong residual parental feeding instinct that continued for a short time after nest failure. This behavior is not uncommon (Welty and Baptista 1988) and, in fact, other bird species have been observed feeding the young of other broods of the same or different species, when their own brood has been destroyed (e.g., Shy 1982, Stafford 1986). Second, since the warblers did not appear to detect the jay near the nest during the removal of the two nestlings, their behavior may have been an attempt to locate, feed, and defend young that could have fledged from the nest while the adults were absent. The nestlings were about 4 days away from fledging, but adult warblers may not be able to accurately predict the timing of this event. Instead, adult warblers may begin the fledgling phase of parental care when they notice that the nestlings are absent from the nest, even if this absence is due to predation.

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Age Differences in Wing Loading and Other Aerodynamic Characteristics of Red-tailed Hawks

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ABSTRACT.—We examined age differences in wing loading, aspect ratio, wing span, and tail area in a sample of 117 Red-tailed Hawks (*Buteo jamaicensis*) captured at the Cedar Grove Ornithological Station, Wisconsin, during 1979–1987. Adults had significantly wider wings, lower aspect ratios, shorter tails, and smaller tail surface areas than juveniles. Red-tailed Hawks showed fewer age differences in aerodynamic characteristics than Sharp-shinned Hawks (*Accipiter striatus*), probably because of differences between the two species in the pursuit and capture of prey. Sharp-shinned Hawks take birds from above ground or after a brief chase, often in dense vegetation. Sharp-shinned Hawks require more aerial agility (ability to make rapid twists and turns) than is necessary for Red-tailed Hawks, which capture prey on the ground, usually after a glide or flight from an elevated perch. Received 7 July 2003, accepted 6 August 2004.

Wing area, wing loading, and other aerodynamic characteristics are especially important for those diurnal birds of prey that spend considerable time on the wing and rely on agility in flight for capturing prey. There are few data on aerodynamics for species of Falconiformes; of the data that do exist, they may include only a single specimen, and often age is not noted (Mueller et al. 2002). We examined age differences in wing loading and other aerodynamic characteristics of Red-tailed Hawks (*Buteo jamaicensis*) based on a sample of 117 wings and 89 tails. We captured the hawks during fall migration 1979–1987 at the Cedar Grove Ornithological Station (43° 33' N, 87° 21' W) on the western shore of Lake Michigan in Sheboygan County, Wisconsin.

The hawks were trapped in bow-nets or dho-gazzas (Bub 1991).

We previously explained in detail (Mueller et al. 1981) the methods used to obtain our data. Briefly, we held up the extended wing (or tail) against a vertical sheet of Plexiglass ruled into 5-cm squares and photographed it. Subsequently, we projected each negative to one-half life size on a sheet of paper and drew an outline of the wing and the adjacent body (or tail). We measured the area of each drawing with a compensating polar planimeter. Measurements were taken as in Mueller et al. (2002): wing surface area is the area of both wings plus the area of the adjacent body; wing loading is mass divided by wing area; flight surface area is wing surface area plus tail surface area; flight surface loading is mass divided by flight surface area; wing span is 2 × wing length plus the distance across the adjacent body; and aspect ratio is the square of the wing span divided by wing surface area. Using SYSTAT for Macintosh (Wilkinson 1989), we conducted *t*-tests for all comparisons.

Tail surface area varies greatly with how much the tail is spread. We used the following formula to estimate tail area, using only angle of spread and tail length:

$$\text{Area} = (A/360) (\pi B^2 - \pi C^2),$$

where A is the angle formed by lines drawn along the two outer rectrices until they meet on a drawing made from a photograph of the tail, B is the distance from the apex of this angle to the tip of the longest rectrix, and C is B minus the tail length measured on the live bird. Regression of C on A yields $C = -0.11A + 16.64$, $R^2 = 0.67$, $P < 0.001$. The surface area thus estimated is an excellent fit to the measured area (adults $R^2 = 0.85$; juveniles $R^2 = 0.89$; both $P < 0.001$).

Juveniles had significantly narrower wings,

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higher aspect ratios, and longer tails than adults (Table 1). The angle of spread of the photographed tails did not differ between juveniles and adults, and at an angle of about 65° juveniles had significantly greater tail surface areas (12.8%) than adults. The difference in tail area ranged from 9.7% in a mostly folded tail (spread 15°) to 13.4% in a fully fanned tail (130°).

There were no significant differences between juveniles and adults in mass, wing loading, or flight surface loading (wing and tail). However, adults had greater mass than juveniles in a larger sample taken during 1963–1999 ($t = 8.64$, $df = 4,398$, $P < 0.001$). Wing surface areas were not measured in the 1963–1999 sample, but age differences in wing loading might exist.

Adults thus had shorter tails, lower aspect ratios, and wider wings than juveniles. The tail of a bird serves a vital function during landing, when it is spread and thrust forward: it deflects air downward over the wings, thus increasing lift and preventing a stall (Pennycuik 1985). This effect would be particularly useful in the high speed “landing” when a hawk strikes prey on the ground. The larger tails of juveniles aid these inexperienced birds in striking prey. The wider wings of adults

may help compensate for their shorter tails. The higher aspect ratio in juveniles makes them more efficient in soaring flight but at the expense of a loss in maneuverability, which is compensated for by an increase in tail area.

Red-tailed Hawks strike their prey on the ground, usually after a glide or flight from an elevated perch (Preston and Beane 1993). Mammals are the hawks' most common prey; during a predation attempt, the maximum aerodynamic constraints a hawk incurs are probably in braking just before the prey is struck. Sharp-shinned Hawks (*Accipiter striatus*) show more age differences in aerodynamic characteristics than Merlins (*Falco columbarius*), which in turn show more differences than Red-tailed Hawks. Sharp-shinned Hawks capture perched birds, often in dense vegetation, or in flight after a brief chase (Bildstein and Meyer 2000). Merlins usually capture birds in the air, often after a series of stoops at a flight speed considerably greater than that of Sharp-shinned Hawks (Sodhi et al. 1993). The tail and wings are used to deflect the airstream in rapid twists and turns. The force produced by such a deflecting surface is proportional to the area of the surface and the square of the airspeed. A falcon in rapid flight needs less deflecting surface than a hawk en-

TABLE 1. Wing chord, wing loading, and other characteristics of Red-tailed Hawks captured during fall migration at Cedar Grove Ornithological Station, Wisconsin, 1979–1987.

	Adults ($n = 52$)		Juveniles ($n = 65$)		t	P^a
	Mean	SD	Mean	SD		
Wing chord (cm)	38.2	1.75	38.4	1.75	0.78	1.00
Wing length (cm)	54.2	2.86	54.8	3.07	1.07	1.00
Wing width (cm)	19.4	1.06	18.7	0.96	3.31	0.01
Wing span (cm) ^b	122.0	5.75	122.5	6.44	0.42	1.00
Aspect ratio ^c	6.31	0.34	6.54	0.30	3.95	0.001
Wing surface area (cm ²) ^d	2364.1	212.9	2298.8	214.5	1.04	1.00
Mass (g)	1083.8	152.8	1064.5	162.4	0.66	1.00
Wing loading (g/cm ²) ^e	0.458	0.049	0.462	0.049	0.44	1.00
Tail length (cm)	21.1	0.96	22.7	1.01	7.30	0.001
Tail angle (degrees) ^f	66.8	12.22	63.4	18.82	0.74	1.00
Tail surface area (cm ²) ^g	440.4	59.66	496.6	85.83	3.49	0.001
Flight surface area (cm ²) ^h	2804.5	212.93	2795.4	214.98	0.23	1.00
Flight surface loading (g/cm ²) ⁱ	0.386	0.041	0.380	0.042	0.79	1.00

^a Bonferroni corrected probabilities.

^b $2 \times$ wing length plus the distance across the adjacent body.

^c Wing span²/wing surface area.

^d Area of both wings, plus the area of the adjacent body.

^e Mass divided by wing area.

^f Angle of spread of the tail. The sample size for tail measurements is 39 adults and 50 juveniles.

^g Tail surface area at 65° angle of spread.

^h Wing surface area plus tail surface area.

ⁱ Mass divided by flight surface area.

gaged in slower twists and turns. Compared with Sharp-shinned Hawks and Merlins, the minimal age-related differences in control surfaces of Red-tailed Hawks may result from a reduced need for them. The variation between species in age differences in aerodynamic characteristics is attributable to differences in hunting methods.

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Breeding Ecology and Nesting Success of Abbott's Babbler (*Malacocincla abbotti*)

Andrew J. Pierce,^{1,2} Korakoch Pobprasert,¹ and George A. Gale¹

ABSTRACT.—Baseline demographic data are lacking for most tropical forest birds, particularly from undisturbed habitats. During the 2003 breeding season, we documented the productivity of Abbott's Babbler (*Malacocincla abbotti*), a sedentary insectivorous passerine, on a 30-ha permanent forest plot in northeastern Thailand. We found 17 active nests of 13 breeding pairs, for which the Mayfield estimate for overall nesting success was 0.36 ± 0.13 SE. Breeding started in mid-January, a month earlier than previously recorded. Despite a relatively long period of post-fledging parental care, at least five pairs were double-brooded. Received 3 February 2004, accepted 11 August 2004.

The breeding ecology and nesting success of many tropical birds is generally unknown (Robinson et al. 2000, Stutchbury and Morton 2001). In Asia, documentation, if any, often only describes the first known nesting, or unusual nesting behavior. Detailed demographic information on tropical birds from relatively undisturbed forest is essential for elucidating questions related to the evolution of life history characteristics, such as clutch size, number of broods, and nest success (Robinson et al. 2000), while at the same time serving as baseline data for assessing how species may respond to the rapid deforestation in the region (Lambert and Collar 2002, Food and Agriculture Organization of the United Nations 2003). We present information on the breeding ecology of Abbott's Babbler (*Malacocincla abbotti*), collected during an intensive study of forest birds in northeastern Thailand.

The Abbott's Babbler is a small, sedentary passerine that ranges from Nepal and north-east India through south-east Asia to Sumatra and Borneo. In Thailand, it is fairly common

in the understory of broad-leaved evergreen forest and secondary growth up to 915 m in elevation (Robson 2000). Abbott's Babbler is socially monogamous with monotypic plumage. Males are larger than females (flattened wing chord: $75.3 \text{ mm} \pm 1.24$ SE, $n = 21$, and $72.8 \text{ mm} \pm 0.80$ SE, $n = 14$, respectively; AJP unpubl. data).

METHODS

Data were collected from January to June 2003 on the 30-ha Mo-singto permanent forest plot, Khao Yai National Park, Nakhon Nayok Province ($14^\circ 26' \text{ N}$, $101^\circ 22' \text{ E}$). The plot was situated in mature, seasonally-wet evergreen forest at 723–817 m in elevation (Brockelman 1998). The vegetation was undisturbed except for a 20×120 m strip of approximately 40-year-old secondary forest at the northern edge of the plot. The average annual rainfall is 2,326 mm, most of which falls between May and October (Kitamura et al. 2002).

We conducted intensive searches to locate nests and breeding pairs of Abbott's Babblers. Nest contents were checked every 2–5 days to estimate laying, hatching, and fledging dates. We caught adult birds in mist nets using song playback or by placing nets near nests after eggs had hatched. Nestlings were banded 6–8 days after hatching. We banded all birds with one aluminum, Thai Royal Forest Department-numbered band and 2–3 color bands to allow individual recognition in the field. We calculated nesting success (incubation and nestling periods) following Mayfield (1961); standard errors were calculated following Hensler (1985).

RESULTS AND DISCUSSION

We found 13 pairs of Abbott's Babblers nesting on the plot; of those, 21 individuals were banded. At least one member of each pair was banded such that each nest could be assigned to a known pair. The banded male of

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TABLE 1. Mayfield estimates for nest success of Abbott's Babbler at Khao Yai National Park in north-eastern Thailand, January–June 2003. Exposure days were terminated at the mid-points between the last observed active and the first observed inactive dates (Mayfield 1961). All nests in the calculations were of known outcome.

	Incubation period (<i>n</i> = 10 nests)	Nestling period (<i>n</i> = 12 nests)	Total (<i>n</i> = 17 nests)
Duration in days	17.75 ^a	11 ^b	28.75
Failed nests	1	7	8
Exposure days	98	96	194
Daily nest survival	0.990	0.927	0.966
Nest success ^c	0.834	0.435	0.362
Standard error ^d	0.152	0.137	0.133

^a *n* = 6 nests, starting from first egg date following Robinson et al. (2000).

^b *n* = 4 nests.

^c Expected nest success based on daily survival rate.

^d Calculated following Hensler (1985).

one pair disappeared after a failed nesting attempt and was replaced by an unbanded bird that did not breed. All other banded individuals remained paired in their territories throughout the study.

We found 17 active nests (8 first nests and 9 renests) of 6 pairs. The renests represented a range of 1–3 additional attempts. Fifteen nests were in rattan palms (*Calamus* spp.) and two were in small unidentified saplings (KP unpubl. data). We found nests from early February to late May, with young fledging from the last nest on 12 June. Two pairs with fledged young on 8 and 9 February, respectively, indicated that egg-laying began in mid-January. This extends by 1 month the previous estimated start date of the nesting cycle (Robinson 2000). Clutch or brood size was three in all but one nest, which was found with two nestlings about 8 days old.

One egg was laid per day and incubation (female only) started the day after the clutch was complete. Of 28 eggs monitored, only 1 failed to hatch. Ten successful nests fledged 29 chicks. The incubation period was 14–15 days (mean = 14.75, *n* = 6) and nestlings fledged 10–12 days after hatching (mean = 11, *n* = 4). The Mayfield estimate for overall nest survival was 0.36 ± 0.13 SE (Table 1). Nest predation, and not desertion, appeared to be the main cause of nest failure; when it occurred, all contents of the nest were depredated. Although we had no direct observations of

predation events, potential predators could have included a variety of other bird species, squirrels, snakes and pig-tailed macaques (*Macaca nemestrina*).

Because the adults were uniquely color-banded, we were able to document that at least five pairs (38%) were double-brooded—i.e., initiated a second nest after having already fledged young from a previous nest, following the definition of Ogden and Stutchbury (1996). For two of these pairs, at least part of their first brood was observed alive, and still dependent on the male, when the second nest was started. Eggs in both second nests hatched and the females attempted to raise their second broods alone; however, both nests failed due to predation. The first eggs of these two second broods were laid 49 and 64 days after first broods fledged. In a third pair, the second nesting attempt was initiated 46 days after the first brood fledged and 10 days after the fledged young were last known to be alive. In the remaining two pairs, first-brood fledglings disappeared within 2 weeks of fledging and presumably died prior to the second nesting attempts.

Our study represents one of the few detailed studies of the breeding biology of a Southeast Asian forest bird. Fogden's (1972) ground-breaking and widely cited study conducted in Sarawak, Malaysia, suggests that species that provide extensive post-fledging parental care (>10 weeks) do not have sufficient time for double-brooding during a normal breeding season. Our data suggest that Abbott's Babblers regularly care for young for 7–9 weeks or more after fledging, and yet are still able to double-brood—enabling them to potentially increase reproductive output (Holmes et al. 1992, Ogden and Stutchbury 1996).

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First Nest Description for the Ocellated Antbird (*Phaenostictus mcleannani*)

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ABSTRACT.—We present the first description of a nest of the Ocellated Antbird (*Phaenostictus mcleannani*), an understory species that ranges from southeastern Honduras to northwestern Ecuador. The open-cup nest was found in June 2002, in the Republic of Panama, and was located on the leaf litter between the buttresses of a *Virola surinamensis* tree. The nest contained two ovoid, whitish eggs with reddish-brown speckles and longitudinal streaks. Received 20 January 2004, accepted 3 August 2004.

The Ocellated Antbird (*Phaenostictus mcleannani*) is a “professional” army ant fol-

lower (*sensu* Willis 1973) that ranges from southeastern Honduras to northwestern Ecuador (Ridgely and Gwynne 1989, Zimmer and Isler 2003). In the Republic of Panama, the Ocellated Antbird is widespread throughout the undergrowth of lowland humid forests and has been recorded at elevations of up to 900 m (Ridgely and Gwynne 1989). Ocellated Antbirds, along with Bicolored Antbirds (*Gymnophithys leucaspis*) and Spotted Antbirds (*Hylophylax naevioides naevioides*), form the core of ant-following assemblages in central Panama (Willis 1973). The Ocellated Antbird is the least common of the three species, is relatively secretive, and is rarely observed away from swarms of army ants (Willis 1973). The natural history of this group is of interest due to its notable vulnerability to habitat fragmentation and isolation; for example, the Oc-

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ellated Antbird became extirpated from Barro Colorado Island in the 1970s (Karr 1982, Robinson 1999). Despite intensive studies of their ecology and behavior (Willis 1973), no confirmed observations of Ocellated Antbird nests have been previously reported. Here, we present what we believe is the first description of this species' nest.

We studied the reproductive ecology of birds on a 104-ha study area (see Robinson et al. 2000 for a full description of the study area) in the lowland forests of Soberania National Park in the Republic of Panama (9° 10' N, 79° 45' W). On 26 June 2000, while checking the buttresses of a medium sized *Virola surinamensis* tree (Family Myristicaceae: ~20 m high, 0.80 m diameter at base of buttresses, and 0.25 m diameter at breast height), AIC flushed an adult Ocellated Antbird and discovered a cup nest built amid the leaf litter on the ground between two of the tree's buttresses. The nest tree was located in forest 60–120 years old (Robinson et al. 2000).

We revisited the nest site on 27 June and measured the nest and eggs. The nest was set on the ground litter and was attached at the rim to the tree buttresses with fungal rhizomorphs (*Marasmius* spp.). The nest itself was a tightly knit cup made from fine fungal rhizomorphs and dried leaves. We did not observe additional lining material. The interior of the cup measured 85 mm in width and 40 mm in depth. The eggs were ovoid and whitish, speckled with reddish-brown spots and longitudinal streaks, much like Bicolored Antbird eggs (Stiles and Skutch 1989). The eggs weighed 5.0 and 4.9 g and both measured 27 mm in length and 20 mm in width at the widest point.

We revisited the nest every 3 days. The nest contained two eggs on 30 June, and on 3 July, we observed two naked hatchlings; their eyes were closed. By 6 July, the hatchlings had feather sheaths, and by 9 July, they were downy and their eyes had opened. On 15 and 16 July, the nest was intact but empty. Although we did not directly observe whether the nestlings fledged successfully or were depredated, a nestling period of approximately 12 days is common for open-cup-nesting antbirds (Willis 1972, Stiles and Skutch 1989).

The nest we observed was similar to descriptions of putative Ocellated Antbird nests

presented by Willis (1973) and Zimmer and Isler (2003). We believe that our observations confirm the Willis (1973) and Zimmer and Isler (2003) nests as those of the Ocellated Antbird.

Most other species in the families Thamnophilidae and Formicariidae attach their open-cup nests to horizontal forks of shrubs or trees (antshrikes, antvireos, some antwrens and antbirds), or build in a hollow or cavity (some antbirds and antthrushes). The Ocellated Antbird's placement of a cup nest on the ground between tree buttresses makes it somewhat unique in these families (Stiles and Skutch 1989, Cadena et al. 2000). Species in the ecologically similar genus, *Phlegopsis*, place their nests inside hollow tree stumps (Cadena et al. 2000). A two-egg clutch is standard for open-cup nesters in the humid tropics (Skutch 1985).

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Ornithological Literature

Edited by Mary Gustafson

WHOSE BIRD?: COMMON BIRD NAMES AND THE PEOPLE THEY COMMEMORATE. By Bo Beolens and Michael Watkins. Yale University Press, New Haven, Connecticut, 2004: 378 + 22 pp. in-text illustrations. ISBN: 030010359X. \$35.00 (paper).—The history of ornithology, probably more than that of any other science, is rich in a spectacular cast of extraordinary characters: rogues, saints, soldiers, sailors, adventurers, misfits, scientists, aristocrats and hoi polloi, liars and frauds, priests and missionaries. This is hardly surprising, considering that the search for new bird species involved travel to places where there was a better-than-average chance of being eaten (by everything from a crocodile to a cannibal), shot, speared, drowned, frozen, or otherwise dispatched to a better world by encountering any one of a variety of unpleasant tropical diseases or large, antisocial wild animals. Many of these remarkable and frequently outright eccentric individuals attained ornithological immortality by having species named after them. *Whose Bird?* is a compendium of “the people behind the bird names.”

The book starts with an entertaining and informative introduction that includes the nuts-and-bolts of how the text is organized. That quickly leads to a dryly hilarious section entitled, *How to Get a Bird Named After You*, subsections of which include *Discovery*, *Identity*, *Other Paths to Glory*, *Forgery and Theft* (regrettably frequent), and *Backscratching* (with useful hints). In *Identity*, the author swiftly reaches the conclusion that those with the best chance of eponymous immortality were typically moneyed, Victorian, and western (later in the text, a table of ‘Olympian’ nationalities shows the British winning the gold, the United States the silver, and the French the bronze). *Other Paths to Glory* suggests that, if you can’t discover a new species by groveling through dense tropical forest in person, you can pay somebody else to do it; or even better, have a royal heritage. Queen Victoria probably had no interest whatsoever

in any birds that weren’t on the plate in front of her, but she still “owns” three species.

The bulk of the book (361 pages to be exact) is given over to an alphabetical list of names associated with bird taxa—not only species, but often races as well, following the now-defunct custom of giving full English names to subspecies. Each entry gives details of the life and history of the “name,” frequently the circumstances of the species’ discovery, and all sorts of other facts—often comic, curious, bizarre, admirable, or deplorable. This section is a treasure-trove of trivia guaranteed to keep the reader anticipating the next entry. For example, did you know that Xantus (of the murrelet and hummingbird) was a pathological liar who built a great reputation among the folks back home in Hungary by wildly exaggerating his adventures in the Wild West, including (though he never served in the U.S. Navy) having himself photographed in the uniform of a U.S. naval captain? That Emin Bey (of the sparrow, shrike, and weaver) was beheaded by African slave-traders? That Richard Bowdler Sharpe (of too many species to mention) had a family of 10 daughters? Or that Sir Harry Johnston (of the turaco) spoke 30 African and several European languages?

One pleasing feature of the book is the inclusion of many portraits or photographs of the “names,” many of whom were impressively hirsute individuals glaring at the camera through an impenetrable thatch of beard and moustache while clutching some fearsome bird-dispatching piece of weaponry. An exception was Père David, who is unarmed, benevolent-looking (as befits a Man of God), and in Chinese costume. Also scattered in among the biographies are miscellaneous treatments on the fates and backgrounds of many “names,” including the following: *Murder* (at least seven ornithological victims); *Shot* (no less than five, most of them by careless handling of muzzle-loading firearms); *Elephant’s Revenge* (at least three met their Maker at the hands, or rather, feet, of irate pachyderms); *Watery Graves* (no less than three); *East India Company*; *Minis-*

ters, Missionaries and Monks; and Charlatans and Cheats (not as rare as you'd think).

Is it possible to criticize this book? There are a few omissions. For example, three of the four subspecies of wrens named after Philip Sclater were omitted, as were three other subspecies of wrens—Branicki's, Bangs', and Cabot's. A study of C. E. Hellmayr's *Birds of the Americas* would undoubtedly turn up others. If we want to be really picky, the year in which Queen Victoria became Empress of India is incorrect (in reality it was not until 1876) and the authors also indicate that Gilbert White's village was Selbourne (but it was Selborne). Minor criticisms aside, *Whose Bird?* is such an entertaining book that one is left with a feeling of regret that it is not longer and does not provide more detail and portraits. For example, Sr. Fermín Cervera was described by Barbour [the naming authority for Zapata Wren (*Ferminia cerverai*)] as a "somewhat peculiar person in several respects." One would love to know how these peculiarities manifested themselves! It is also a source of some regret in this particular reviewer that Elliot Coues' character assessment of Dr. Thomas Brewer (of the sparrow and blackbird) as a "cantankerous old ass" didn't quite make it in! Brewer, incidentally, was one of the few ornithologists of his time who supported the introduction of the House Sparrow (*Passer domesticus*) into North America.

The compilation of this book, the authors themselves admit, "started off as a bit of fun." It has resulted in a book that most certainly is fun to read, and if you are looking for a Christmas present for someone, look no further. The book, however, is also a serious and significant addition to the ornithological literature and should be recommended to anyone with an interest in the colorful history of field ornithology.—DAVID BREWER, Puslinch, Ontario, Canada; e-mail: mbrewer@albedo.net

OKLAHOMA BREEDING BIRD ATLAS. Edited by Dan L. Reinking. University of Oklahoma Press, Norman, Oklahoma. 2004: 528 pp., 222 color illustrations, 230 color maps. ISBN: 0806136146. \$34.95 (paper).—The first North American breeding bird atlases

were initiated during the 1970s. With atlases completed or ongoing in more than 40 U.S. states and most Canadian provinces, these projects are now familiar to professional ornithologists and amateur birders. This book provides the results of the *Oklahoma Breeding Bird Atlas*, the data for which were collected during 1997–2001. Its appearance less than 3 years after completing fieldwork is remarkable and everyone associated with its timely publication should be congratulated for their efforts.

This atlas provides the first comprehensive summary of Oklahoma breeding bird distribution since George M. Sutton's *Oklahoma Birds* was published in 1967. Its format is similar to that of other published atlases. The 8-page introduction describes the Oklahoma atlas, summarizes its coverage and limitations, provides a brief overview of results, and lays the foundation for the species accounts. The second chapter provides a 5-page summary of the major vegetative communities in Oklahoma and briefly discusses the climatological and geological factors influencing the distribution of vegetation and birds. The remaining text is largely devoted to accounts of the 212 species detected during the atlas project. Each species account has a standardized, 2-page layout, including an introductory paragraph, a brief description of the species, and summaries of its breeding habitats occupied in Oklahoma, nesting ecology, rangewide distribution, historic and current status in Oklahoma, population trends from the North American Breeding Bird Survey, and references. An attractive color photograph of the species accompanies each account, and a color map depicts the distribution of the species' atlas records. These maps are fairly small, but the color scheme effectively presents the distributional data (assuming the reader is not red-green color blind). The appendices include brief descriptions of the status of extinct, extirpated, irregular, and potential breeding species not treated in the species accounts, and provide examples of field data forms. A 36-page bibliography supports the cited literature.

Oklahoma is a large state with a birding community concentrated near the few large cities. Hence, atlas organizers emphasized thorough coverage of a smaller number of pri-

ority blocks rather than spreading efforts thinly over more blocks. Only one priority block in every two 7.5-minute USGS topographic quads was covered for this atlas. This decision did not affect distribution patterns of widespread species but allowed only fragmentary coverage for rare or locally distributed species. Data from other sources were used to fill the gaps for species not well-represented by the atlas coverage. Limiting distribution discussions to single paragraphs on historic and current status did not allow for detailed summaries of this information. While these paragraphs tend to be fairly brief, generally they successfully convey current status and historic changes in distribution. Unfortunately, this publication did not take advantage of breeding bird atlas data from surrounding states to provide a broader geographic context for recent distributional changes detected in Oklahoma.

The *Oklahoma Breeding Bird Atlas* is a well-produced book that reflects very favorably upon everyone who collected data, contributed to the species accounts, and coordinated the project. This atlas will undoubtedly become the benchmark against which future changes in Oklahoma breeding birds are measured. Anyone with an interest in the avifauna of this state or the Great Plains region should obtain a copy.—BRUCE G. PETERJOHN, USGS Patuxent Wildlife Research Center, Laurel, Maryland; e-mail: Bruce.Peterjohn@usgs.gov

LIFE ON MATAGORDA ISLAND. By Wayne H. McAlister, illustrated by Martha K. McAlister. Texas A&M University Press, College Station, Texas. 2004: 244 pp., 10 chapters, 50 hand drawn illustrations, 1 map. ISBN: 1585443379 / 1585443387. \$35.00 (cloth), \$17.95 (paper).—Situated along the central Texas coast, Matagorda Island is one of two very lightly developed barrier islands in Texas. The island is about 64 km in length and provides significant wetland resources, including habitat for its most well-known occupant, the Whooping Crane (*Grus americana*).

The book is a narration of many observations made by the author when employed as a naturalist on Matagorda Island National

Wildlife Refuge. Most observations pertain to living on a remote barrier island and the daily activities of numerous invertebrate and lower vertebrate species that inhabit the island's varied habitats. Some of the species discussed are coquina (*Donax variabilis*), mole crab (*Emerita portoricensis*), tiger beetle (*Cicindela dorsalis*), ghost crab (*Ocypode quadrata*), burrowing sea cucumber (*Leptosynapta inhaerens*), striped mullet (*Mugil cephalus*), mud fiddler crab (*Uca pugnax*), mosquito (*Aedes* spp. and *Psorophora* spp.), valentine ant (*Crematogaster lineolata*), amphioxus (*Branchiostoma guanhuami*), gooseneck barnacle (*Lepas anatifera*), and rainbow dung beetle (*Phanaeus difformis*). I recommend that students and researchers read this book prior to visiting a barrier island.—BRENT ORTEGO, Texas Parks and Wildlife Department, Victoria, Texas; e-mail: Brent.Ortego@tpwd.state.tx.us

THE SIBLEY FIELD GUIDE TO BIRDS OF EASTERN NORTH AMERICA. By David A. Sibley. Alfred A. Knopf, New York. 2003: 433 pp., numerous color illustrations and range maps. ISBN: 067945120X. \$19.95 (paper); and **THE SIBLEY FIELD GUIDE TO BIRDS OF WESTERN NORTH AMERICA.** By David A. Sibley. Alfred A. Knopf, New York. 2003: 473 pp., numerous color illustrations and range maps. ISBN: 0679451218. \$19.95 (paper).—With this pair of books, Sibley has answered the critics of *The Sibley Guide to Birds* (2000, Alfred A. Knopf, New York) who liked the illustrations and text but disliked the book's size. In his preface, Sibley indicates that his decisions about the content in each of these volumes reflected the need to keep these volumes "accurate and complete while also portable and easy-to-use." The size of these books (12 × 19.5 cm), addresses the issue of portability quite well. As with his earlier guide, the illustrations are outstanding. His illustrations of birds performing a variety of behaviors are particularly useful because posture and behavior can be as important to identification of many species as field marks.

These two volumes are not simply *The Sibley Guide to Birds* in two halves; rather, they

are two field guides that may meet the needs of birders of various levels of experience over a wide geographic range. The eastern guide covers species that are found in states and provinces east of the Rocky Mountains and the western guide covers species that are found west of the Rocky Mountains. Despite the designation of eastern and western regions, each guide covers a large percentage of North American birds—650 species in the eastern guide and 703 species in the western guide. In addition to coverage of indigenous species, a number of exotic species—including waterfowl, game birds, parrots, and finches—receive treatment in these guides.

The guides are easy to use, with species accounts that provide multiple images of most species, including profiles of birds perched and in flight. Illustrations show age-related, sexual, seasonal, and/or geographic variations in plumage and are accompanied by lines of text that point out features that may be important in identification. Each account also includes a brief description of general abundance, habitat, social behavior, feeding habits, distinguishing markings and/or behaviors, and vocalizations. Species' range maps include summer, winter, and year-round distributions, as well as areas where birds are regularly seen during migration or dispersal. The maps also indicate where a species has been seen on rare occasions. I was pleased that the range maps in both field guides encompass a given species' entire North American range (excluding southern Mexico), which will allow most birders to travel with only one of the two volumes.

As in *The Sibley Guide to Birds*, the eastern and western guides include overviews of most taxonomic groups. Sibley also provides comparisons of easily confused groups or species. These treatments, for both individual species and groups, are less extensive than they are in *The Sibley Guide to Birds*. For example, the Herring Gull (*Larus argentatus*) account in *The Sibley Guide to Birds* includes 13, 11, and

2 illustrations of American, Vega (Siberian), and European birds, respectively, and a diagram of the long call behavior. In the eastern guide, however, there are 9 illustrations of American Herring Gulls, and in the western guide there are 10 illustrations of American and 2 of Vega Herring Gulls (non-breeding adults). The eastern and western guides cover many rare visitors, but illustrations of these are limited and range maps are not included (although geographic location is covered in the text).

The introductions in each field guide include an introduction to birding and birding ethics; information about bird classification and taxonomy; molt, plumage, and variations in how birds may appear; learning songs and calls; finding rare birds; extinct species; and conservation. The treatment of variation in appearance covers a range of topics, including geographic variation and subspecies, polymorphism, wear and fading, changes in posture and head shape, lighting and atmospheric conditions, staining, aberrant plumages, bill deformities, and hybrids. The section on bird topography is extensive, providing diagrams of passerines, gulls, ducks, and shorebirds. The treatment of passerines also includes several diagrams of head feathers, body feathers, and wing feathers. The diagrams are the same as those used in *The Sibley Guide to Birds*, but the written descriptions are substantially reduced to allow for all the diagrams. Font sizes throughout the two guides are necessarily small to facilitate the inclusion of substantial amounts of information without crowding, but some readers may find the small size frustrating.

Overall, I found these books to be user-friendly, extremely well illustrated, and portable. Sibley's field guides will be useful for bird watchers at a variety of skill levels, and I enthusiastically recommend them.—SARA R. MORRIS, Canisius College, Buffalo, New York; e-mail: morriss@canisius.edu



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FRONTISPIECE. Five members of the Tribe Ardeini (Great Blue Heron, *Ardea herodias*; Yellow-crowned Night-Heron, *Nyctanassa violacea*; Snowy Egret, *Egretta thula*; Little Blue Heron, *Egretta caerulea*; and Black-crowned Night-Heron, *Nycticorax nycticorax*) whose ornamental plumes emerge during the later stages of the definitive prebasic molt; Pyle and Howell found no evidence for a prealternate molt. Original painting (watercolor gouache on acrylic) by Barry Kent MacKay.

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ORNAMENTAL PLUME DEVELOPMENT AND THE “PREALTERNATE MOLTS” OF HERONS AND EGRETS

PETER PYLE^{1,3} AND STEVE N. G. HOWELL²

ABSTRACT.—To investigate molts and ornamental-plume development in herons and egrets, we examined 48 specimens of 10 North American species. We found no evidence for a prealternate molt, despite widespread opinion that such a molt occurs and includes the ornamental plumes. Our data indicate that these plumes emerge during the later stages of the definitive prebasic molt in August–November, grow slowly through January–February, and are retained until replacement during the following prebasic molt. The preformative (traditionally termed “first-prebasic”) molt shows substantial variation in extent. In 91.9% of 86 first-year individuals collected between November and May, this molt included the development of ornamental plumes that were similar in form, but shorter in length, than those of adults. Male Great Blue (*Ardea herodias*) and Little Blue (*Egretta caerulea*) herons developed longer ornamental plumes than females, presumably a result of sexual-selection strategies. *Received 9 February 2004, accepted 28 September 2004.*

Herons and egrets (Tribe Ardeini) are widely regarded as having two plumages per year—a “non-breeding” or basic plumage in fall and winter, and a “breeding” or alternate plumage in spring and summer (Palmer 1962, Cramp 1977, Hancock and Kushlan 1984, Marchant and Higgins 1990, Voisin 1991). The extent of “pre-breeding” or prealternate body-feather molts reportedly varies from at least a few crown feathers in Great Blue Heron (Palmer 1962; see Table 1 for scientific names) to complete in Great Egret, Cattle Egret, and Black-crowned Night-Heron (Witherby et al. 1939). The ornamental plumes have been considered part of the alternate plumage, with shorter basic ornamental plumes reportedly being replaced by longer alternate plumes in spring (Palmer 1962, Telfair 1994).

By definition, the occurrence of a prealter-

nate molt requires the activation of follicles more than once during the molt cycle (Humphrey and Parkes 1959). In north-temperate herons and egrets, therefore, an early spring molt (additional to the annual prebasic molt) has been presumed, involving the replacement of basic ornamental plumes along with varying proportions of basic contour feathers. In order to confirm the existence of prealternate molts and determine the occurrence and length of basic and alternate ornamental plumes in herons and egrets, we examined 448 specimens of the 10 species that breed in North America north of Mexico.

METHODS

Specimens of herons and egrets were examined at the California Academy of Sciences (CAS), San Francisco; the Museum of Vertebrate Zoology (MVZ), Berkeley; the British Museum of Natural History, Tring; the American Museum of Natural History, New York; and the B. P. Bishop Museum, Honolulu. All specimens were collected in Canada, the United States, and northern Mexico, presumably

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TABLE 1. Number of North American heron and egret specimens examined and proportion of each sample collected during active molt, by season and age.^a

Species	Age ^a	Jul–Aug <i>n</i> (%)	Sep–Oct <i>n</i> (%)	Nov–Dec <i>n</i> (%)	Jan–Feb <i>n</i> (%)	Mar–Apr ^b <i>n</i> (%)	May–Jun ^b <i>n</i> (%)	Total ^c <i>n</i> , <i>n</i>
Great Blue Heron (<i>Ardea herodias</i>)	AD	3 (0.3)	8 (0.9)	7 (0.1)	7 (0.0)	25 (0.0)	17 (0.1)	67, 13
	1Y	3 (0.0)	5 (0.2)	5 (0.4)	13 (0.2)	7 (0.0)	2 (0.0)	35, 6
Great Egret (<i>Ardea alba</i>)	AD	5 (0.2)	5 (1.0)	5 (0.4)	3 (0.0)	8 (0.0)	1 (0.0)	27, 8
	1Y	3 (0.0)	7 (0.4)	3 (0.3)	3 (0.3)	1 (0.0)	4 (0.0)	21, 5
Snowy Egret (<i>Egretta thula</i>)	AD	2 (1.0)	0 (—)	4 (0.3)	1 (0.0)	4 (0.0)	3 (0.0)	14, 3
	1Y	6 (0.0)	5 (0.4)	0 (—)	0 (—)	3 (0.0)	2 (0.0)	16, 2
Little Blue Heron (<i>Egretta caerulea</i>)	AD	5 (0.6)	3 (1.0)	2 (0.0)	5 (0.0)	5 (0.0)	7 (0.3)	27, 8
	1Y	0 (—)	0 (—)	0 (—)	1 (0.0)	2 (0.0)	3 (0.0)	6, 0
Tricolored Heron (<i>Egretta tricolor</i>)	AD	2 (1.0)	1 (1.0)	2 (0.5)	3 (0.0)	1 (0.0)	2 (0.0)	11, 4
	1Y	2 (0.0)	4 (0.5)	2 (0.0)	2 (0.0)	1 (0.0)	1 (0.0)	12, 2
Reddish Egret (<i>Egretta rufescens</i>)	AD	2 (0.0)	1 (1.0)	4 (0.3)	1 (0.0)	6 (0.0)	2 (0.5)	16, 3
	1Y	1 (0.0)	4 (0.3)	2 (0.5)	1 (0.0)	0 (—)	2 (0.0)	10, 2
Cattle Egret (<i>Bubulcus ibis</i>)	AD	3 (1.0)	0 (—)	3 (0.0)	2 (0.0)	2 (0.0)	4 (0.3)	14, 4
	1Y	0 (—)	0 (—)	6 (0.3)	0 (—)	1 (0.0)	6 (0.0)	13, 2
Green Heron (<i>Butorides virescens</i>)	AD	9 (0.8)	7 (0.9)	2 (0.0)	2 (0.0)	6 (0.0)	6 (0.0)	32, 13
	1Y	6 (0.0)	6 (0.2)	1 (0.0)	0 (—)	3 (0.0)	6 (0.0)	22, 2
Black-crowned Night-Heron (<i>Nycticorax nycticorax</i>)	AD	7 (0.6)	5 (1.0)	5 (0.2)	6 (0.0)	7 (0.0)	7 (0.1)	37, 11
	1Y	2 (0.0)	10 (0.2)	7 (0.1)	6 (0.5)	4 (0.0)	5 (0.0)	34, 6
Yellow-crowned Night-Heron (<i>Nyctanassa violacea</i>)	AD	4 (0.8)	6 (0.8)	0 (—)	1 (0.0)	2 (0.0)	4 (0.5)	17, 10
	1Y	4 (0.0)	5 (0.6)	3 (0.0)	3 (0.3)	0 (—)	2 (0.0)	17, 4
Total	AD	42 (0.6)	36 (0.9)	34 (0.2)	31 (0.0)	66 (0.0)	53 (0.2)	262, 77
	1Y	27 (0.0)	46 (0.3)	29 (0.3)	29 (0.3)	22 (0.0)	33 (0.0)	186, 31

^a Ages are coded as AD (adult) and 1Y (first-year); see text for definitions.

^b For first-year birds in April–June, the proportion represents those undergoing the preformative molt. First-year birds that had commenced the second prebasic molt (as indicated by the shedding of the first primary; see text) were not considered as being in active preformative molt.

^c The total column includes the overall specimen sample and the sample collected in active molt.

from populations with boreal breeding and molt cycles. For each specimen, we assigned age and sex based on plumage and information on the specimen label. Birds were aged as either “first-year” (in their calendar year of hatching or through June of the following year) or “adult” (at least 1 year older than first-year) through examination of plumage, shape of the outer primaries and rectrices, and presence or absence of replacement patterns among the secondaries and primaries (Palmer 1962, Cramp 1977, Baker 1993; specimen examination by PP). First-year birds do not replace juvenal primaries, whereas adults often show wear patterns indicating gradual replacement. Juvenal outer primaries and rectrices are narrower and more pointed than those of adults, and body plumage and wing coverts of darker-plumaged herons show age-specific differences in color patterns. Individuals that showed equivocal or conflicting characters ($n = 19$ of 467, particularly among white-plumaged egrets) were excluded from the sample. Sex designations reported on specimen la-

bels—presumably based on internal examination—were assumed to be correct.

We categorized specimens as actively molting if contour feathers (excluding ornamental plumes) or flight feathers were growing. Contour feathers throughout all body tracts were carefully lifted and examined for pins or developing feathers (cf. Johnson 1963). In specimens not actively molting when collected ($n = 340$), occurrence and extent of contour-feather molts were assessed by examining the proportion of replaced feathers that were markedly fresher than juvenal or basic feathers, considering the duration of the previous prebasic molt and temporal period since its completion. Fewer than five new contour feathers were assumed to represent adventitious replacement (e.g., after accidental loss) rather than molt. Although flight-feather replacement patterns can be complicated in herons (cf. Shugart and Rohwer 1996), flight-feather molt can be an accurate temporal marker for prebasic molt; e.g., we considered the second prebasic molt to have commenced

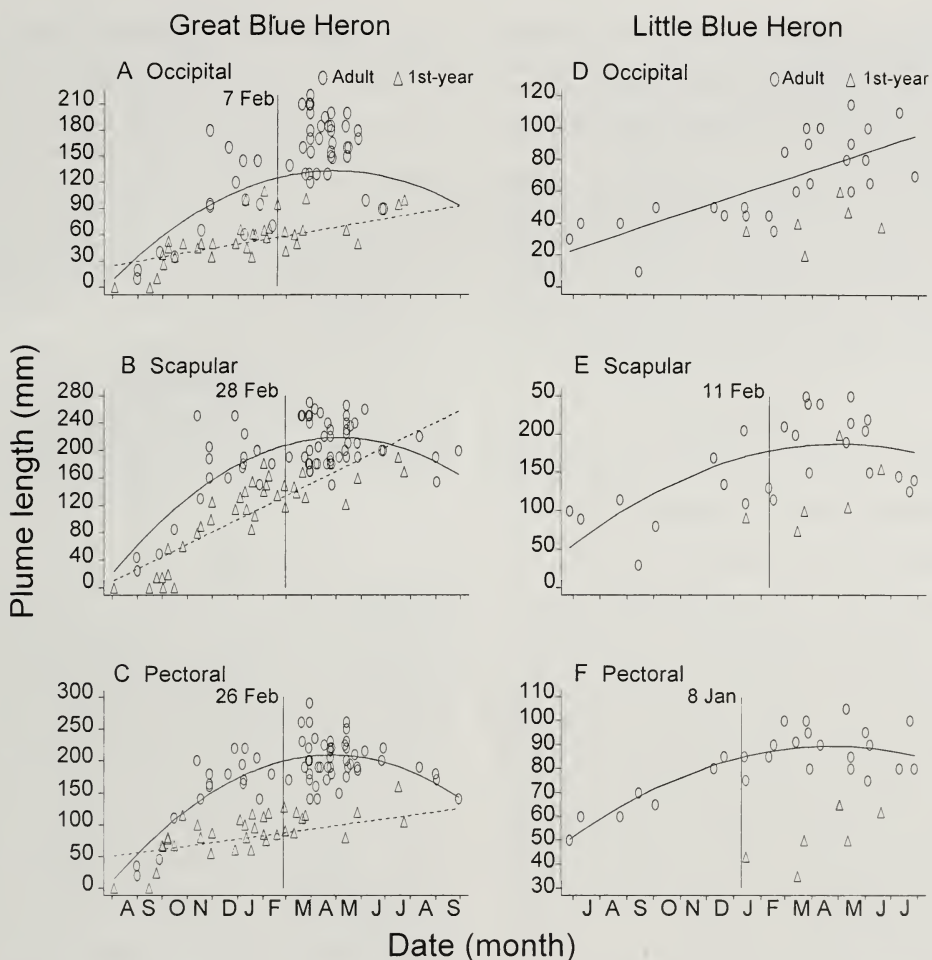


FIG. 1. Occipital, scapular, and pectoral plume lengths by month (Julian date) and age in Great Blue and Little Blue herons, indicating slow rate of growth and lack of replacement during winter and spring. Curvilinear regression lines (adult herons) are shown where quadratic terms were significant (see text); otherwise, linear regressions (dashed for first-year Great Blue Herons, solid for adult Little Blue Herons) are shown. Vertical lines represent the estimated date at which plumes attain full length within the population (95% of the maximum value of the fitted quadratic curves). Sample size ($n = 6$) for first-year Little Blue Herons was insufficient for meaningful regression analysis.

when the innermost juvenal primary had been shed.

To assess the growth rate of ornamental feathers at the population level, we measured—from insertion to tip—the longest occipital, scapular, and pectoral plumes in adult Great Blue and Little Blue herons. Specimens on which the longest plume appeared to be missing or broken were excluded. Growth of ornamental plumes was estimated using linear and non-linear regression of plume length against Julian date and a quadratic date term (date^2), respectively, the latter to estimate the

curvilinear rate of growth (see Seber and Wild 2003 for use of quadratic terms in regression). Julian dates were based on a starting point of 1 June to include the subsequent prebasic molt, and an ending point of 30 September to include the prior prebasic molt, thus ranging from 1 to 487 (15 months). We estimated the completion of plume development as the date by which the fitted quadratic curve had reached 95% of its maximum value (see Fig. 1). Unless specified, results of non-linear regression are reported when the quadratic term was significant; otherwise, results of linear re-

gressions are reported. Sex-specific differences in plume lengths were assessed using Analysis of Variance (ANOVA). Statistics were performed using the program Stata (Stata Corporation 1997).

Molt and plumage terminology follows Humphrey and Parkes (1959) except for that of the first molt cycle, in which we use the terms "formative plumage" (in lieu of the traditional term "first basic plumage") and "preformative molt" (in lieu of "first prebasic molt") following Howell et al. (2003).

RESULTS

Molts in herons and egrets.—Of 448 aged individuals, 186 were first-year birds and 262 were adults (Table 1). Among adults, active prebasic molt occurred in birds collected from 15 June to 23 November ($n = 77$). Among first-year birds, active preformative molt occurred from 14 September to 24 February ($n = 29$). The second prebasic molt had commenced in 12 of 33 birds collected between 28 April and 30 June, the date after which first-year birds were reclassified as adults (Table 1). No active contour-feather molt was detected in 97 adults collected in January–April (Table 1), and no evidence of partial prealternate molts was detected in 70 adults collected between April and the onset of the subsequent prebasic molt (May–August).

Fourteen adults (7 Great Blue Herons, 1 Snowy Egret, 2 Reddish Egrets, 3 Little Blue Herons, and 1 Cattle Egret) were in the process of replacing ornamental plumes when collected. In all 14 specimens, short new plumes were in pin or were emerging adjacent to retained old plumes. These specimens were collected between 17 August and 23 November during the later stages of active prebasic flight-feather and contour-feather molt. On the Cattle Egret, the older plumes were tawny and the newer plumes were white.

In first-year birds, the preformative molt showed substantial variation in extent. In 29 individuals collected between 1 March and commencement of the second prebasic molt, the extent of replacement ranged from most feathers of the head and neck and a few scapulars (Great Blue Heron MVZ15554), to all or nearly all body feathers, all lesser and median coverts, five proximal secondaries (including the tertials), and five medial rectrices (Green

Heron CAS24684). Ornamental plumes were developed as part of this molt, as evidenced in 91.9% of 86 first-year individuals collected between November and May, before the onset of the second prebasic molt. These formative plumes were similar in form to those of adults but were shorter in length (Fig. 1; see below). The lack of a prealternate molt during first and later molt cycles and the timing and extent of preformative molt were similar among all 10 taxa (Table 1).

Ornamental plume lengths in Great Blue and Little Blue herons.—Our data indicate that the ornamental plumes of adult Great Blue and Little Blue herons emerged in September or October during the prebasic molt (see above) and continued to grow through January or February, after which growth ceased (Fig. 1). For all three plume types of Great Blue Heron ($n = 47$ –58; Fig. 1A–C), and for scapular ($n = 22$; Fig. 1E) and pectoral ($n = 26$; Fig. 1F) plumes of Little Blue Heron, growth rates were negatively curvilinear ($t < -2.79$, $P < 0.008$ for four analyses, and $t = -0.201$, $P = 0.056$ for scapular plume length in Little Blue Heron), indicating decelerated or arrested growth during the summer and early fall. Estimated dates for attainment of full plume length varied from 8 January to 28 February (Fig. 1), and were earlier in Little Blue Heron (8 January to 11 February) than in Great Blue Heron (17–28 February). Plume length of adults appeared to shorten during June–October, presumably due to wear. Growth of occipital plumes in adult Little Blue Herons was linear ($t = 5.48$, $P < 0.001$; $n = 26$) but not curvilinear ($t = -0.063$, $P = 0.54$) with respect to date, suggesting continued growth through the summer (Fig. 1D). There was no indication that plumes in either species were replaced at any time other than during the prebasic molt (Fig. 1).

In first-year Great Blue Herons, for which sample size ($n = 35$) was sufficient to perform regression analyses, plume lengths showed significant linear trends for all three plume types ($t > 4.03$, $P < 0.001$; Fig. 1A–C), but non-significant curvilinear trends in two of three types ($t > -1.20$, $P > 0.065$ for occipital and pectoral plumes; $t = 4.62$, $P < 0.001$ for scapular plumes), generally indicating continued growth of preformative plumes into the spring.

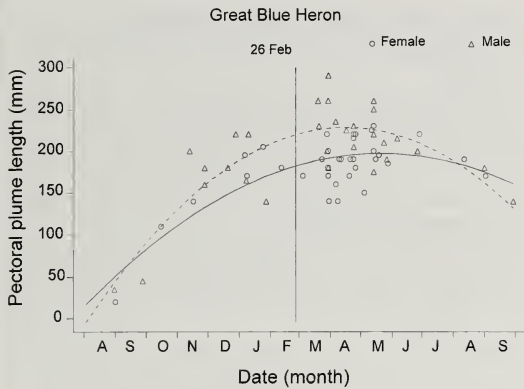


FIG. 2. Pectoral plume length by month for male and female Great Blue Herons, showing greater plume lengths of males (dashed curvilinear regression line) than females (solid line).

In adults, full-grown plumes (on dates following those on which the fitted quadratic curve had reached 95% of its maximum value; Fig. 1) were longer in males than in females and this comparison was significant for all three plume types of Great Blue Heron (ANOVA: $F > 6.79$, $P < 0.013$, $n = 49\text{--}58$) and for pectoral plumes in Little Blue Heron ($F = 4.15$, $P = 0.046$, $n = 26$). For example, mean pectoral plume length of male Great Blue Herons from 26 February to 27 September (Fig. 2) was 217.8 mm (95% CI = 146–290, $n = 20$), whereas mean pectoral plume length of females was 190.3 mm (95% CI = 138–242, $n = 29$). When dates were restricted to 26 February to 15 May (before the effects of feather wear obscure sex-specific differences; see Fig. 2), mean pectoral plume length was 231.2 mm for males (95% CI = 171–291, $n = 10$) and 182.6 mm for females (95% CI = 135–231, $n = 19$).

DISCUSSION

Our results suggest that herons and egrets lack a prealternate molt, despite widespread opinion to the contrary. There was no evidence of active contour-feather replacement among 167 adults collected between January and the onset of the prebasic molt (as early as 15 June). Direct specimen examination and growth-curve data indicate that ornamental plumes emerge during the later stages of the definitive prebasic molt in August–November, grow slowly through January–February, and

are kept until replaced during the next prebasic molt. A slow rate of growth has also been documented for ornamental feathers of tropicbirds (Veit and Jones 2004), indicating that such feathers may require substantial resources to produce; thus, it seems both unlikely and unnecessary that these feathers would be replaced twice per year.

Herons and egrets thus exhibit the Complex Basic Strategy of molt as defined by Howell et al. (2003), as do other species (e.g., bitterns and tiger-herons) within Ardeidae (Palmer 1962; specimen examination by PP and SNGH). We believe that ornithologists concluding that a prealternate molt existed in herons and egrets have been misled by (1) the slow growth of ornamental plumes in adults—not reaching full length or becoming apparent in the field until winter or early spring; (2) the protracted preformative molts, which usually include growth of ornamental plumes on first-year birds into the following spring; and (3) a plumage color change during spring in at least one species, the Cattle Egret.

Molt in Cattle Egret was examined by Siegfried (1971) and discussed by Telfair (1994). Siegfried's data indicated that this species may have only one molt per year and that new white ornamental plumes replaced old pigmented plumes after the breeding season; however, he did not discuss these findings in relation to molts in Ardeini. Telfair critiqued Siegfried's study and proposed a molt strategy involving a prealternate molt that included longer alternate ornamental plumes replacing shorter basic plumes. Although our sample size of Cattle Egrets was small, our study indicates only a single replacement of ornamental plumes during the prebasic molt, as in other herons and egrets. As first suggested by Humphrey and Parkes (1963) and later discussed by Telfair (1994), the ornamental plumes of Cattle Egrets appear to gain pigmentation by staining derived from the uropygial gland or topical deposition of carotenoids, rather than through replacement of plumes. Our examination of 14 adult Cattle Egret specimens supports this supposition: none showed evidence of a prealternate molt, and color saturation of the pectoral and scapular plumes generally became darker in a clinal manner (with individual variation; cf. Mad-

dock 1989) as date of collection progressed from winter through spring.

Our study also indicates that male herons and egrets develop longer ornamental plumes, at least on average, than females. This is the first evidence for sex-specific plumage differences among North American Ardeini and suggests that longer plumes in males than in females are due to sexual-selection strategies. It is possible that these differences are greater than those we report, due to mis-sexed individuals in our sample (cf. Parkes 1989). We suggest that more comprehensive analyses or models, using a combination of all plume lengths and date on individuals of confirmed sex, may produce methods for the accurate sexing of adult herons and egrets during spring.

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FEMALE BROWN-HEADED COWBIRD WITH PARTIAL MALE PLUMAGE

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ABSTRACT.—There are few records of functionally female birds exhibiting partial to total male plumages. On 26 March 2004, we collected a female Brown-headed Cowbird (*Molothrus ater*) at Fort Hood, Texas, with a presumably functional ovary and whose back and belly exhibited the glossy, greenish-black plumage typical of after-hatch-year males. This individual is a unique specimen because (with the exception of partial albinism) no aberrant plumages have been reported for Brown-headed Cowbirds. Received 27 May 2004, accepted 16 October 2004.

Fort Hood, an active military installation located in central Texas (Bell and Coryell counties), practices Brown-headed Cowbird (*Molothrus ater*; hereafter cowbird) control as a means of reducing brood parasitism on endangered songbirds that nest on the installation (Eckrich et al. 1999). On 26 March 2004, a cowbird with an unusual plumage was trapped at Fort Hood. The head and breast of this bird were brownish-gray (i.e., typical female coloration; Fig. 1). Although individual and groups of feathers on its back and belly were also brownish-gray, its back and belly were predominately a glossy, greenish-black typical of after-hatch-year males (Pyle 1997). Upon dissection, we discovered that the cowbird had a reduced (i.e., follicles were small, approximately 1 mm in diameter, and white), but presumably functional, ovary on its left side. Wing chord (104 mm) and tail (71 mm) measurements were consistent with the cowbird being a large *M. a. artemisiae* female (Pyle 1997).

Females that exhibit partial to total male plumages are rare but have been reported for Northern Bobwhite (*Colinus virginianus*; Buchanan and Parkes 1948), American (*Falco sparverius*; Parrish et al. 1987) and Lesser (*F. naumanni*; Tella et al. 1996) kestrels, Bay-breasted Warbler (*Dendroica castanea*; Stoddard 1921), and Spotted Towhee (*Pipilo maculatus*; Bergtold 1916). Male-like feather pigmentation can result from hormonal abnormalities. Andersson (1994) suggested that both sexes carry the genes that influence sec-

ondary sexual characteristics, and expression of these genes is related to sex-specific hormones (i.e., estrogen and testosterone). Further, Owens and Short (1995) suggested that the showier breeding plumage of males of many species is actually the neutral stage of development and that more cryptic female plumages are induced by estrogen production. Thus, the male plumage characteristics observed on our female cowbird could have resulted from reduced hormone secretion. Alternatively, the observed plumage may be the result of a genetic abnormality. Cowbirds maintain similar-looking plumage year-round; therefore, hormones may not have a large influence on feather pigmentation (Lowther 1993, Owens and Short 1995, Pyle 1997).

Regardless of the mechanism responsible for its aberrant plumage, the cowbird we collected is a unique specimen. With the exception of partial albinism (Stewart 1963), few unusual plumages have been reported for cowbirds (Lowther 1993, Ortega 1998). Further, we have trapped and destroyed >19,512 female cowbirds at Fort Hood during 1999–2003 (The Nature Conservancy of Texas, Fort Hood, unpubl. data), and none of the birds exhibited unusual plumages. We deposited our cowbird specimen (FMNH 440412) at the Field Museum of Natural History, Chicago, Illinois.

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FIG. 1. Female Brown-headed Cowbird (*Molothrus ater*) trapped at Fort Hood, Texas, on 26 March 2004, exhibiting brownish-gray head and breast typical of females, but a predominately glossy, greenish-black back and belly typical of after-hatch-year males. Photograph by D. A. Cimprich.

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AGE STRUCTURE OF NEOTROPICAL MIGRANTS DURING FALL MIGRATION IN SOUTH DAKOTA: IS THE NORTHERN GREAT PLAINS REGION AN INLAND “COAST”?

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ABSTRACT.—Proportions of juvenile birds in migrant populations at coastal stopover sites are often higher than proportions of juveniles at inland stopover sites, a phenomenon called the “coastal effect.” The northern Great Plains forms the western boundary of the migratory ranges for many Neotropical woodland migrants. Moreover, woodland habitat is scarce in this region, consisting primarily of natural riparian corridor woodlands (hereafter corridors) and planted woodlots and shelterbelts around farmsteads and agricultural fields (hereafter woodlots). Due to the scarcity of woodland habitat, one might expect that adults—by virtue of their experience and better-developed navigational abilities—would avoid the Great Plains during fall migration, thus producing age structures in migrant populations similar to those found at coastal sites. We tested this “inland coast” hypothesis for Neotropical migrants captured during fall migration at corridor and woodlot stopover sites in southeastern South Dakota. We classified migrants into three groups based on whether our South Dakota study sites were peripheral (western edge of migratory range within South Dakota), near-peripheral (western edge in, or just west of, Wyoming or Montana), or central (western edge well west of Montana and Wyoming) to their regular migratory ranges. We captured higher juvenile proportions of peripheral ($86.5 \pm 10.4\%$, 2 species) and near-peripheral ($85.6 \pm 4.5\%$, 7 species) migrants than central migrants ($79.6 \pm 7.2\%$, 5 species), but the difference was not significant ($P = 0.11$). The proportion of juveniles was inversely correlated with the distance of our study sites from the western edge of a given species’ migratory range ($r = 0.476$, $P = 0.085$). The proportion of juvenile Neotropical migrants at our study sites was near the upper end of proportions recorded for other inland sites in North America, but was slightly lower than those recorded at coastal sites. Our results are, therefore, only partially consistent with the inland coast hypothesis, suggesting that factors other than geographic location also shape age structures at our study sites. The mean proportion of juveniles (for species captured ≥ 13 times in both habitats; $n = 10$) was significantly greater ($P = 0.002$) in the woodlot ($89.1 \pm 7.0\%$) than in corridors ($73.8 \pm 12.5\%$). The differential age structure in the two habitats suggests that habitat characteristics may influence age structure of the migrant community, but mechanisms for such an influence are currently unknown. Received 5 August 2003, accepted 21 October 2004.

Variation in age structure among Neotropical migrants at stopover sites during migration may indicate age-related differences in the selection of migration routes (Clench 1969, Ralph 1981), timing of migration (Drury and Keith 1962, Hussell et al. 1967, Stewart et al. 1974, Hall 1981), or navigational abilities (Drury and Keith 1962, Ralph 1978). Ralph (1971, 1978) proposed that age-related differences in migratory orientation abilities and experience may lead to a higher-than-expected incidence of juvenile birds at coastal sites or at the peripheries of migratory routes, a so-called “coastal effect.” Most of the data

supporting these conclusions were derived by comparing age structures and densities at coastal stopover sites with similar data from interior sites (Drury and Keith 1962; Murray 1966; Ralph 1971, 1978, 1981). Subsequent research has confirmed the generally high proportion of juveniles at coastal stopover sites (Hall 1981, Stewart 1986, Taylor et al. 1994, Morris et al. 1996, Woodrey and Moore 1997). Ralph (1981) further argued that sites with higher percentages of juveniles and lower overall densities were principal criteria for defining the periphery of a species’ migration route. This argument implies that the causative factor for the high proportions of juveniles at coastal sites is that they are peripheral to the main migratory route for the species. The basis for this argument is the unproven assumption that following a main migratory route is an adaptive behavior, and that individuals straying from these routes suffer increased mortality, and thereby reduced fitness (Ralph 1981). The coastal effect could also

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result from young birds seeking out coastal habitats for a variety of reasons (e.g., better food resources, decreased competition with adults, navigational purposes). None of these alternatives has been adequately addressed and the causative factors underlying the coastal effect are not well understood. If, however, Ralph's (1981) assumption—that the periphery of a migratory route confers lower fitness—is valid, and juveniles occur in higher proportions at the periphery due to less effective navigation, then the proportion of juveniles at the periphery of a species' migratory route should be high relative to more-central sites, whether coastal or inland.

Age structures during fall migration have been documented for several inland sites (Ralph 1971, 1978, 1981; Stewart et al. 1974; Hall 1981; Rimmer and McFarland 2000), but none of these sites lies near the inland boundary of the migratory ranges for migrants typically associated with forested areas in eastern North America. Consequently, the age compositions of fall migrants at inland peripheries of routes are essentially unknown. The northern Great Plains lies on the western periphery of migratory routes used by a number of eastern migrants (American Ornithologists' Union 1998). Current landscapes of the eastern portion of the northern Great Plains consist mainly of agricultural habitats interspersed with pastures and grasslands. Woodland habitats in this region are scarce, composing only about 4% of land area in southeastern South Dakota. Historically, they consisted mainly of natural, deciduous riparian woodlands bordering streams and rivers (hereafter corridors), but they have since been supplemented with woodlots and shelterbelts surrounding farmsteads and agricultural fields (hereafter woodlots). Of the current woodland area in southeastern South Dakota, 60 and 40% is composed of woodlots and corridors, respectively (Castonguay 1982). If adult birds are capable of more refined orientation during migration than juveniles, then it might be expected that they would avoid the relatively inhospitable landscapes of the northern Great Plains, which would result in age structures skewed toward juveniles in this region. As a consequence, age structures of migratory populations in this area might resemble coastal age structures, at least for those species for which the northern

Great Plains are peripheral to the main migratory range. A corollary prediction of the coastal effect hypothesis is that the proportion of juveniles should be greater in migratory populations of peripheral species than central species.

We evaluated the age structure of Neotropical migrant passerines captured at corridor and woodlot study sites during fall migration in southeastern South Dakota to delineate age-related migratory patterns in the northern Great Plains. Our objectives were to determine (1) whether coastal-like proportions of juveniles occurred at these study sites, (2) whether the proportion of juveniles in migrating populations differed between peripheral and central species, and (3) whether proportions of juveniles differed between corridor and woodlot study sites—the two habitats that represent the major types available to woodland migrants seeking stopover sites in this area.

METHODS

Study sites.—We captured Neotropical migrants with mist nets (9 × 2.6 m, 30 mm mesh) at four corridor sites in Clay and Union counties in southeastern South Dakota during fall migration (15 August–6 October) from 1993 through 1995. Three of the study sites were located in riparian corridor habitats along the Missouri and Big Sioux rivers. The fourth study site was located on a north-south tributary of the Big Sioux River (Bule Creek), and included both upland and riparian deciduous habitats. Migrants were also captured with mist nets at a single farmstead woodlot study site (~3.5 ha) during fall migration (15 August–6 October) in 1996 and 1997. These study sites and their vegetation are described in detail in Dean (1999) and Swanson et al. (2003). Because we sampled in corridor and woodlot study sites in different years, between-year differences might confound comparisons of age structure between sites; however, Ralph (1981) showed that 2 years of intensive sampling produced juvenile percentages within 5% of long-term averages for 95% of all species. Because we sampled intensively for at least 2 years at each study site, our data should accurately reflect the long-term age structure of migrants at these sites. Moreover, early August to early October

TABLE 1. Percent juveniles and total captures (*n*) for Neotropical migrant species (≥ 15 overall captures) at corridor and woodlot stopover sites in southeastern South Dakota, 1993–1997.

	Corridor		Woodlot		Overall
	%	<i>n</i>	%	<i>n</i>	%
Central migrants					
“Traill’s” Flycatcher (<i>Empidonax traillii</i> and <i>E. alnorum</i>)	60.8	51	91.2	34	72.9
Swainson’s Thrush (<i>Catharus ustulatus</i>)	81.8	11	75.0	4	80.0
Orange-crowned Warbler (<i>Vermivora celata</i>)	69.5	141	75.0	196	72.7
Nashville Warbler (<i>Vermivora ruficapilla</i>)	83.8	74	92.5	199	90.1
Wilson’s Warbler (<i>Wilsonia pusilla</i>)	70.5	44	85.9	142	82.3
Near-peripheral migrants					
Least Flycatcher (<i>Empidonax minimus</i>)	50.0	16	89.1	55	80.3
Red-eyed Vireo (<i>Vireo olivaceus</i>)	83.7	43	100.0	13	87.5
Tennessee Warbler (<i>Vermivora peregrina</i>)	0.0	1	95.8	24	92.0
Yellow-rumped Warbler (<i>Dendroica coronata</i>)	81.8	22	85.9	64	84.9
Black-and-White Warbler (<i>Mniotilta varia</i>)	70.0	10	90.9	11	81.0
Ovenbird (<i>Seiurus aurocapilla</i>)	87.5	16	91.7	24	90.0
Northern Waterthrush (<i>Seiurus noveboracensis</i>)	78.3	23	92.3	13	83.3
Peripheral migrants					
Mourning Warbler (<i>Oporornis philadelphia</i>)	69.0	29	83.9	62	79.1
Canada Warbler (<i>Wilsonia canadensis</i>)	100.0	5	90.9	11	93.8

encompasses the major migration period for both adults and juveniles of most species of Neotropical woodland migrants that move through southeastern South Dakota, except perhaps, for later-migrating individuals of late migrants, such as Orange-crowned (*Vermivora celata*) and Yellow-rumped warblers (*Dendroica coronata*; Tallman et al. 2002).

Capture techniques.—Mist nets were placed at specific locations within each study site during fall migration; the same net locations were used throughout the study (both within and between years) at both corridor and woodlot study sites. Weather permitting, mist-netting was conducted 7 days per week at corridor sites and at least 6 days per week at the woodlot site. We opened 5–7 nets at each corridor site and 7–10 nets in the woodlot site; net hours were recorded as one net open for 1 hr = 1 net-hr. We sampled corridors only in the morning (sunrise until approximately 11:00 CST), whereas we sampled the woodlot in mornings and often evenings (for 2–3 hr prior to sunset) as well (Dean 1999, Swanson et al. 2003). Mist-netting at corridor sites occurred on a 4-day rotation so that each site was visited every 4th day—except during fall 1995, when flooding prevented continuous access to the Big Sioux River site. During the period of flooding, we alternated between the

two Missouri River study sites and the Brule Creek site on alternate days. Nets were not opened on rainy or very windy days. Total net-hr were 2,050 for corridor sites and 5,107 for the woodlot site (Dean 1999, Swanson et al. 2003).

Age structure analysis.—All birds were aged (hatching year = HY, after hatching year = AHY) by skull ossification, which is a reliable aging technique through at least the month of September for most Neotropical migrant passerines (Pyle 1997). For analysis of the “inland coastal effect,” we classified migrants into three groups (peripheral, near-peripheral, and central) based on the degree to which our study sites were peripheral to their regular migratory range (Table 1). Division of migrant birds into these groups was based on the broad-scale migratory range maps in Sibley (2000) and the finer scale migration maps in Tallman et al. (2002). If the western border of the main migratory range fell within South Dakota, we classified species as peripheral migrants; if the western border of the main migratory range at the latitude of South Dakota fell in, or just west of Wyoming or Montana, we classified species as near-peripheral migrants; and, if the western border of the main migratory range fell well west of Montana and Wyoming, we classified species as central mi-

grants. Yellow-rumped Warbler was classified as a near-peripheral migrant because the Myrtle race (*D. c. coronata*) is a common fall migrant in eastern South Dakota, but is rare in western South Dakota and casual in western North America away from coastal wintering areas (Hunt and Flaspohler 1998, Tallman et al. 2002). We did not include migrants that regularly breed at our study sites because we could not reliably distinguish between local breeders and passage migrants from farther north. Grouping species into arbitrary associations (e.g., by migratory boundaries) introduces difficulties in analyses such as these because each species has range boundaries that are not identical to those of other species, and which may vary temporally. However, because we were interested in broad-scale patterns of age structure that should apply generally to migrants—depending on the relative degree to which our sites are peripheral to the migratory range—we contend that pooling species into these groups does provide an adequate test of the “inland coast” hypothesis.

Migratory group comparisons.—We analyzed differences in juvenile proportions among migratory groups by calculating the percentage of juveniles for individual species captured ≥ 15 times and then calculating means for each group. Percentage data were arcsine-transformed prior to calculating means and we used one-way ANOVA to compare group means. Because only two species of peripheral migrants met the criterion of ≥ 15 captures, the power of one-way ANOVA to detect differences among means was very low. Consequently, we also compared mean juvenile proportions of pooled peripheral and near-peripheral migrants (means for the two groups were essentially identical, see Results) with central migrants by *t*-test.

We also calculated Pearson's correlation coefficients to test for correlations between proportions of juveniles at our study sites and distance to the edge of the migratory range. To determine distance to migratory range edge, we measured the approximate distance (nearest 50 km) to the migratory border (from maps in Sibley 2000) for each species at the latitude of our study sites (43° N) with the Geodetic II World Distance Calculator program, ver. 1.0 (www.infoairports.com/freeservices/worlddistance.html). For the Myrtle race of the Yellow-rumped

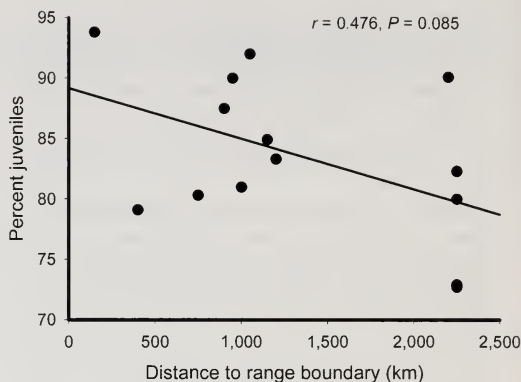


FIG. 1. Correlation between proportion of juveniles (species captured ≥ 15 times) for pooled corridor/woodlot sites and distances from our study sites to the approximate western boundaries of species' migratory ranges.

Warbler, whose migratory range Sibley (2000) depicts as extending west to the west coast of North America (where it is only a casual fall migrant *away from the coast*; Hunt and Flaspohler 1998), we arbitrarily selected the western border of Wyoming as the edge of its migratory range. Changing the western edge of the migratory range for this species by 500 km in either direction resulted in a maximum change of only 0.012 in the Pearson's correlation coefficient, so the exact position of the migratory boundary had little impact on our results.

Comparisons with other sites.—We used paired *t*-tests to compare mean proportions of juveniles for species that occurred at both our study sites (corridors and woodlot pooled) and other inland sites (see Fig. 1). We also calculated Pearson's correlation coefficients to test for correlations between latitude and proportions of juveniles at inland and coastal study sites. Latitudes for other study sites in North America, when not reported, were estimated (to the nearest 0.5° N) with the Geodetic II World Distance Calculator program.

Between-habitat comparisons.—For each migratory group, we used *t*-tests to compare mean percentages of juveniles in corridor sites versus the woodlot site [calculated for species captured ≥ 15 times in each habitat, but also including Red-eyed Vireo (*Vireo olivaceus*) and Northern Waterthrush (*Seiurus noveboracensis*), captured ≥ 15 times in corridors but only 13 times in the woodlot]. For between-habitat comparisons of juvenile proportions by

individual species (using only those species captured ≥ 15 times), we used a log-likelihood ratio for 2×2 contingency tables (G statistic, Zar 1996).

Additional statistics.—Median migration dates were established for species with ≥ 6 captures for each age class. Age-related synchrony of migration was compared using a median test 2×2 contingency table, which was analyzed by chi-square or Fisher's Exact tests (Zar 1996). Statistical significance for all tests was set at $P < 0.05$, except for paired t -tests of species that occurred at both our sites and other inland sites, and G -tests and median tests on individual species where multiple significance tests were required. For these tests, we used a sequential Bonferroni procedure (Rice 1989) to adjust α -levels and reduce the probability of type 1 errors, with $k = 7$ for paired t -tests, $k = 8$ for between-habitat comparisons for individual species, and $k = 6$ in both corridors and woodlots for median tests for individual species. Means are presented \pm SD.

RESULTS

Migration timing.—One factor influencing the variability of age structures at stopover sites may be age-related asynchrony in migratory timing. If sampling effort is not even over the entire migration period, or if peak migratory periods for specific age groups are undersampled, then calculations of age structures may be inaccurate (Kelly and Finch 2000). The age structures we report are not a reflection of asynchronous migration, as median migration dates of adults and juveniles did not differ ($P > 0.05$, all species).

Migratory group comparisons.—The proportions of juveniles (for species with ≥ 15 captures, Table 1) for peripheral migrants ($86.5 \pm 10.4\%$, $n = 2$ species), near-peripheral migrants ($85.6 \pm 4.5\%$, $n = 7$ species), and central migrants ($79.6 \pm 7.2\%$, $n = 5$ species) did not differ ($F_{2,11} = 1.474$, $P = 0.27$). The proportion of juveniles was higher for peripheral and near-peripheral migrants pooled ($85.8 \pm 5.3\%$) than for central migrants, but not significantly so ($t_{12} = 1.73$, $P = 0.11$). Twelve species of peripheral migrants were represented by fewer than 9 captures (48 individuals total): Yellow-bellied Flycatcher (*Empidonax flaviventris*), Eastern Phoebe

(*Sayornis phoebe*), Great Crested Flycatcher (*Myiarchus crinitus*), Blue-headed Vireo (*Vireo solitarius*), Philadelphia Vireo (*Vireo philadelphicus*), Golden-winged Warbler (*Vermivora chrysoptera*), Chestnut-sided Warbler (*Dendroica pensylvanica*), Magnolia Warbler (*D. magnolia*), Black-throated Green Warbler (*D. virens*), Blackburnian Warbler (*D. fusca*), Bay-breasted Warbler (*D. castanea*), and Scarlet Tanager (*Piranga olivacea*). The pooled proportion of juveniles for these 12 species was 93.8%. The proportion of juveniles was inversely correlated (marginally; $r = 0.476$, $P = 0.085$) with the distances of our study sites from the edges of species' migratory ranges (Fig. 1).

Comparisons with other sites.—The proportion of juveniles captured in South Dakota fell within the range (corridor sites) or were near the upper end (woodlot site) of proportions recorded at other inland sites in North America (Fig. 2). Comparisons of shared migrant species revealed that South Dakota study sites had higher proportions of juveniles than all other inland sites, but in only one case was the difference significant (South Dakota versus Carlisle, PA; Table 2). Ralph (1981) considered individual species to exhibit coastal age ratios if the percentage of juvenile birds was $\geq 85\%$. For species with at least 13 captures in our study, coastal-like age ratios ($\geq 85\%$) were obtained for only 1 of 10 species in corridor sites, but for 9 of 11 species in the woodlot site (Table 1). The proportion of juveniles was not correlated with latitude for either inland ($r = 0.43$, $P = 0.25$) or coastal ($r = 0.07$, $P = 0.92$) sites (Fig. 3).

Between-habitat comparisons.—The proportion of juveniles was greater in the woodlot than in corridors for both peripheral/near-peripheral ($t_{10} = 2.82$, $P = 0.018$) and central ($t_6 = 2.55$, $P = 0.044$) migrants (pooled: 73.8 \pm 12.5% juveniles in corridors, 89.1 \pm 7.0% juveniles in woodlots; $t_{18} = 3.55$, $P = 0.002$; Fig. 4). Of the species captured ≥ 15 times in both corridors and the woodlot ($n = 8$ species), only "Traill's" Flycatcher (*Empidonax traillii* and *E. alorum*; $G = 8.76$, $P = 0.004$) and Least Flycatcher (*E. minimus*; $G = 8.42$, $P = 0.004$) differed in age structure between corridors and the woodlot: for both species, there were greater percentages of juvenile birds in the woodlot than in corridors.

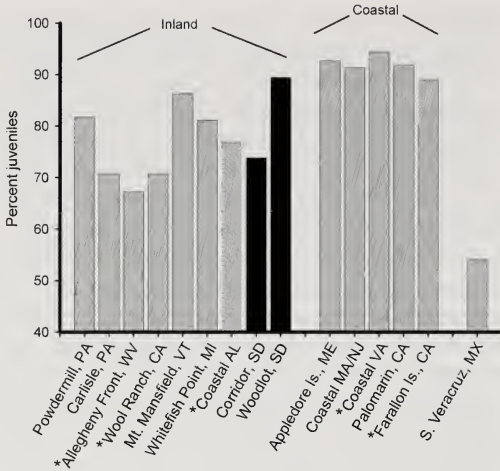


FIG. 2. Age structure of Neotropical woodland migrant populations at inland sites, coastal sites, and southern Veracruz, Mexico. Sites marked with asterisks do not represent the entire Neotropical migrant population, but studies at those sites included at least six commonly captured species of Neotropical migrants. Sites and data sources are as follows: Powdermill and Carlisle, PA, and coastal MA/NJ (Ralph 1981); Allegheny Front, WV (Hall 1981); Wool Ranch and Farallon Islands, CA (Stewart et al. 1974); Mt. Mansfield, VT (Rimmer and McFarland 2000); Whitefish Point, MI (R. Utych pers. comm.; data from fall migration seasons 1995–1997); coastal Alabama (Woodrey and Moore 1997); corridor and woodlot sites, SD (this study); Appledore Island, ME (Morris et al. 1996); coastal VA (Stewart 1986); Palomarin, CA (Taylor et al. 1994); and Veracruz, MX (Winker 1995). The coastal Alabama stopover site was included with the inland sites because it is far removed from the Atlantic coast and lies directly south of inland migration routes. The Veracruz site is unique due to the extreme narrowing of the continental landmass at that location, and is presented separately from inland and coastal sites.

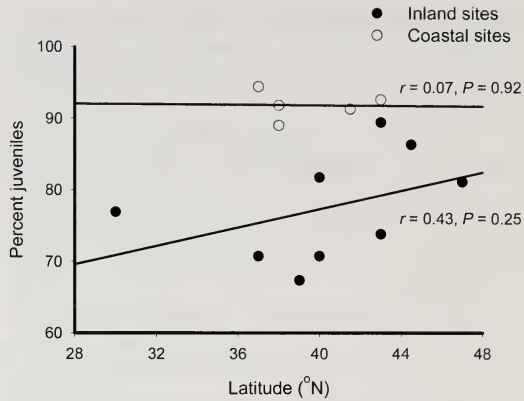


FIG. 3. Correlation between latitude and proportion of juveniles for nine inland and five coastal stopover sites in North America. There was no relationship between latitude and proportions of juveniles at either inland or coastal sites. Sources of data are the same as those listed for Figure 1.

DISCUSSION

Migratory group comparisons.—The proportions of juveniles among peripheral and near-peripheral migrants were slightly greater than they were for central migrants. The proportion of juveniles was inversely related to the distance of our sites from the boundaries of their migratory ranges ($P = 0.085$). Capture rates (this study) and abundance estimates from point counts (Dean 1999, Swanson et al. 2003) of peripheral and near-peripheral species also were typically lower than those for central migrant species, which is one of the criteria proposed by Ralph (1981) for delineating the periphery of a species’ migratory range. The pooled proportion of juveniles for

TABLE 2. Comparisons of mean proportions of juveniles (% HY \pm SD) common to South Dakota (pooled corridor and woodlot data) and seven other inland sites to the east of South Dakota. Comparisons were limited to Neotropical migrant species with ≥ 15 captures/site.

Site ^a	n ^b	% HY	South Dakota % HY	t	P
Powdermill, PA	11	75.1 \pm 13.8	84.6 \pm 4.6	2.26	0.048
Carlisle, PA	10	69.3 \pm 13.3	84.6 \pm 4.9	3.56	0.006 ^c
Allegheny Front, WV	3	70.1 \pm 5.1	88.1 \pm 5.1	9.51	0.011
Mt. Mansfield, VT	7	84.9 \pm 15.3	88.3 \pm 4.7	0.02	0.99
Whitefish Point, MI	13	81.9 \pm 14.4	84.4 \pm 6.0	0.45	0.66
Coastal AL	2	79.1 \pm 11.2	83.8 \pm 5.3	1.16	0.45
Southern Veracruz, MX	3	61.5 \pm 19.5	86.6 \pm 3.9	2.17	0.16

^a For sources of data, see Fig. 1.
^b Number of species occurring at both South Dakota sites and other sites.
^c Significant after sequential Bonferroni adjustment.

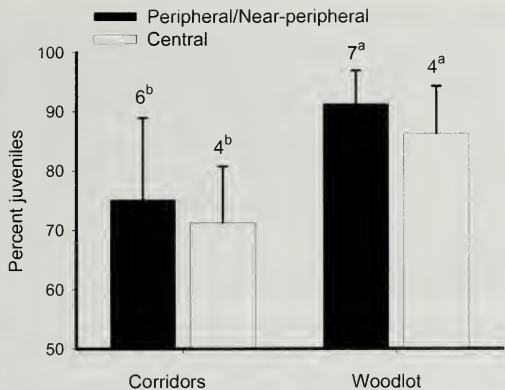


FIG. 4. Proportions of juveniles at corridor and woodlot sites, by two migratory groups, calculated using only species captured ≥ 15 times in both habitats (but also including Red-eyed Vireo and Northern Waterthrush, both of which were captured only 13 times in the woodlot). Sample sizes (number of species) are shown above bars. Bars with different letters (a, b) indicate significant differences ($P < 0.05$).

12 rarely captured species of peripheral migrants was 93.8%, similar to proportions of juveniles at coastal locations. Taken together, these data provide modest support for the inland coastal effect hypothesis.

Comparisons with other sites.—The proportions of juveniles at our study sites, especially at the woodlot, were at the upper end of proportions recorded at other inland sites in North America—also consistent with the inland coast hypothesis. Juvenile proportions for Neotropical migrant populations range from 91.3 to 94.4% HY birds at sites on both the east and west coasts of North America and from 67.3 to 86.3% HY birds at other inland sites (Fig. 2). However, relatively few species in our study had $\geq 90\%$ HY birds—a proportion commonly found at coastal sites. Our data, then, are not wholly consistent with our hypothesis of an inland coastal effect during fall migration whereby adults avoid the northern Great Plains. This suggests that geographic position relative to the main migratory range is not the only factor shaping age structure at inland stopover sites. Less extreme avoidance of the northern Great Plains than of coastal sites by adult birds makes some sense in terms of selection pressures on migrants. Although the northern Great Plains offer little favorable stopover habitat for woodland migrants, the fitness consequences of straying

over this region are not as overtly negative as those of straying over the open ocean.

The proportions of juvenile birds at several inland sites—including those in our study—were greater than the predicted 50–80% of fall populations based on clutch sizes and survival (Ralph 1981). While age structures at inland sites are not as heavily skewed toward juveniles as those at many coastal sites, in several cases inland and coastal sites showed only relatively minor differences. Potential explanations for the higher-than-expected incidence of juveniles at inland sites may include some or all of the following: high breeding productivity (e.g., double-brooding) of migrants (e.g., Holmes et al. 1992), high adult or low juvenile mortality, or lack of age-structure data from a sufficient number of inland sites to provide an accurate overall picture of geographic variation in age structure of eastern migrants. Further study is needed to distinguish between these possibilities.

Variation in age structure among sites might also be explained by differential mortality among age-classes. Annual mortality is highest for migrant birds during migration, and may account for up to 85% of annual mortality in some species (Silleet and Holmes 2002). Juveniles are thought to suffer heavy mortality rates during their first migration, especially when migrating over geographic barriers (Ralph 1978, Gauthreaux 1982, Goss-Custard et al. 1982, Moore et al. 1995). If juvenile mortality is higher than adult mortality during fall migration, then age structure should be more skewed toward adults with increasing distance along the migratory route. However, age structure was not significantly correlated with latitude for either coastal or inland sites in North America, suggesting little differential mortality among age classes.

Another possible method for indirectly assessing juvenile mortality during fall migration is to compare juvenile proportions for species at our study sites with those at stopover sites farther to the south, and therefore farther along the migratory route. Ceilometry data suggest that fall migrants in southeastern South Dakota adopt southeasterly headings (Dean 1999), which, if held constant, would lead them to coastal sites in southern Alabama or Mississippi, and then over or around the Gulf of Mexico. Juvenile proportions were

only slightly higher in southeastern South Dakota than in coastal Alabama (Woodrey and Moore 1997; Fig. 2). Moreover, for the two migrant species that occurred at both our study sites and the coastal Alabama study site, juvenile proportions were 87.5 and 87.0% (Red-eyed Vireo) and 80.0 and 71.9% (Swainson's Thrush, *Catharus ustulatus*) at South Dakota and Alabama sites, respectively. However, the proportion of juveniles was greater at our study sites than at the Isthmus of Tehuantepec in southern Mexico (Winker 1995). These data are consistent with similar mortality of adults and juveniles en route from South Dakota to Alabama, but higher juvenile mortality later in migration. Alternatively, this pattern might be explained by the unlikely possibility that fewer adults than juveniles make trans-Gulf flights (thereby bypassing the Isthmus of Tehuantepec), or by en route recruitment of juveniles along the migratory route. In any event, these data do not provide strong evidence for a high rate of juvenile mortality contributing to the difference in juvenile proportions among inland stopover sites.

Between-habitat comparisons.—Juvenile proportions were generally greater in the woodlot site than in corridor sites. Such a pattern could potentially arise from differences in habitat quality between corridors and woodlots. Vegetational structure and diversity differ among the two habitats: woodlots are generally small, isolated from each other, and exhibit low plant diversity; corridors are generally much larger, more contiguous, and have higher diversity (Dean 1999, Swanson et al. 2003). Because of these differences, corridors might be expected to provide better stopover habitat than woodlots. If corridors are better habitat for migrants than woodlots, then the previous experience and more refined navigational abilities of adult birds (Ralph 1981) would lead us to expect higher densities of adults than juveniles at corridor sites. This tendency could strengthen if adults competitively displace juveniles from corridor sites. If adults preferentially occupy higher-quality stopover sites, then juveniles might occur in greater proportions at lower-quality sites throughout the migratory range. Such a relationship could help explain the coastal effect (if coastal sites are generally inferior to inland

sites) and the relatively wide variation in proportions of juveniles at inland sites (Fig. 2).

Competition for food among migrants can occur at stopover sites and may be more intense where migrant densities are greater (Moore and Yong 1991, Kelly et al. 2002). The relatively small total area of corridor habitats in southeastern South Dakota might concentrate migrants at these sites, thereby increasing competition. However, densities of migrants were roughly similar at corridor and woodlot sites (Swanson et al. 2003). In addition, migrants were generally able to gain mass during stopover at the woodlot (Carlisle 1998, Swanson et al. 2003); thus, woodlots appear to serve as suitable stopover habitat. Inasmuch as relative stopover habitat quality at these sites has not been assessed directly, the contribution of habitat quality to differences in age structure is unknown. Moreover, the absence of marked age-related differences in rates of mass gain (Morris and Glasgow 2001, Jones et al. 2002) suggests that age-related competition may not be a major factor influencing age structures at stopover sites under most circumstances. Thus, the mechanisms responsible for differences in age-structure of migrants between corridors and woodlots in our study are unknown.

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GRIT-SITE SELECTION OF BLACK BRANT: PARTICLE SIZE OR CALCIUM CONTENT?

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ABSTRACT.—We examined selection of grit-ingestion sites by Black Brant (*Branta bernicla nigricans*) on South Humboldt Bay, California in relation to particle size and calcium content. We hypothesized that Brant site selection was dependent primarily upon calcium content and secondarily upon distribution of substrate particle size. We (1) mapped grit-ingestion sites, (2) ranked their importance by Brant abundance and individual movement probabilities between sites, (3) characterized Brant gizzard grit and compared it with grit available at ingestion sites, and (4) compared calcium content and particle-size distribution between ingestion sites and unused sites, and between primary and secondary ingestion sites. Brant repeatedly congregated at specific, discrete sites during the 2 years of observation. The distribution of gizzard-grit particle size was right-skewed toward larger particles (>0.5 mm) relative to the proportional availability of particle sizes in the substrate. We found no significant differences in calcium content or particle size between sites where grit was ingested and unused sites. Within used sites, the calcium content of substrates at the primary ingestion site was significantly higher than at the secondary ingestion sites, as ranked by Brant abundance and between-site movement probabilities. Our findings from the field corroborate previous laboratory results, and confirm that calcium is a significant ecological factor for this species. Received 14 May 2004, accepted 19 October 2004.

Preferred sites for gizzard-grit ingestion may be used faithfully by wild bird populations for many decades (McIlhenny 1932), but site selection of this resource is understudied. It has long been accepted that gizzard grit (hereafter grit) is an essential aid for grinding food (Leopold 1931), and captive birds deprived of grit experience elevated mortality (McCann 1939). In some waterfowl, amount of grit in the gizzard and size of grit particles are related to diet, with more grit and smaller particles in the gizzards of herbivores compared to omnivores and carnivores (Thomas et al. 1977, Skead and Mitchell 1983). Leopold (1933) proposed that grit could be a source of mineral calcium for birds. This is well-documented only for Ring-necked Pheasant (*Phasianus colchicus*), a species whose grit consumption is driven primarily by the need for calcium and only secondarily as a grinding material (McCann 1939)—and whose distribution and abundance is influenced by the availability of calciferous grit (Leopold 1931; McCann 1939, 1961; Dale

1954). Calcium is a crucial breeding-season nutrient for eggshell and skeleton formation, but historically it has been relatively neglected compared with investigations of fat and protein (Alisauskas and Ankney 1992, but see Ankney 1984). Geese rely to varying degrees upon endogenous reserves for successful breeding (Ankney and MacInnes 1978, Raveling 1979, Prop and Black 1998), and although Black Brant (*Branta bernicla nigricans*) rely on reserves less than other arctic-breeding waterfowl of similar mass (Ankney 1984), Brant skeletal mass (an index of calcium content) is reduced 27% between pre- and post-laying (Ankney 1984). Trost (1981) reported that grit consumption by captive female Mallards (*Anas platyrhynchos*) peaks in the spring pre-breeding period; Mallards demonstrate selectivity in both particle size and calcium content. Additionally, a calcium-deficient diet reduces the breeding success of Great Tits (*Parus major*; Graveland and Drent 1997), implying that calcium may be important to breeding birds across taxa.

Here, we examine selection of grit-ingestion sites by Black Brant on South Humboldt Bay, California. Our objective was to examine how calcium and particle size affect site use by Brant, hypothesizing that selection of grit-ingestion sites was dependent primarily upon calcium content and secondarily upon the frequency distribution of particle size. We (1)

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mapped Brant grit-ingestion sites; (2) ranked site importance by Brant abundance and individual movement probabilities between sites; (3) characterized gizzard grit from two time periods, and compared it with grit available at ingestion sites; and (4) compared calcium content and frequency distribution of particle size between ingestion sites and unused sites, and between primary and secondary ingestion sites.

METHODS

Study species and site.—The Black Brant is a small sea goose that breeds and molts in western and northern Alaska, Russia, and the Northwest Territories (Reed et al. 1998). In fall, most Black Brant stage at Izembek Lagoon, Alaska, before migrating south, non-stop, to coastal lagoons of Washington, Oregon, California, Baja California, and Mexico (Reed et al. 1998). During winter and spring, Brant head north again toward breeding grounds in the western Nearctic (Reed et al. 1998). Northward migration is composed of shorter, stepping-stone flights between stopovers at bays and estuaries along the west coast of North America (Reed et al. 1998). We conducted our study at South Humboldt Bay, California (Fig. 1), an important stopover site for Black Brant during their northward migration to the breeding grounds (Moore et al. 2004). Brant begin arriving at Humboldt Bay in mid-December, peak at ~14,000 birds in mid-March, and before April the majority have departed Humboldt Bay (U.S. Fish and Wildlife Service unpubl. data).

Humboldt Bay is a 62-km² estuary (Barnhart et al. 1992); 1,044 ha of eelgrass (*Zostera marina*) occurs in discrete beds interlaced with a dendritic network of channels. Black Brant feed almost exclusively on eelgrass during the non-breeding season, and because Brant do not dive, eelgrass can only be accessed at low tides (Derksen and Ward 1993). South Humboldt Bay contains 70% of the eelgrass beds found in Humboldt Bay, and supports 78–94% of the Brant that use Humboldt Bay each year (Moore et al. 2004). From 350 km to the south to 600 km to the north, Humboldt Bay is the only large estuary containing substantial beds of eelgrass (>300 ha)—effectively making it an insular study area with low

potential for regional movements (Moore et al. 2004).

South Spit, the sandy peninsula separating South Humboldt Bay from the Pacific Ocean, has one large and many small intertidal sandbars along its eastern shoreline that are used by Brant to rest, preen, and ingest grit as the tide ebbs (Fig. 1). These sandbars are exposed early in the ebb, long before the water level is low enough to allow Brant access to the eelgrass beds. As soon as the substrate is within ~0.3 m of the water surface, Brant flock to the sandbar sites to ingest grit.

Observations.—We conducted 88 Brant surveys of South Bay to identify and map the principle grit-ingestion sites. In 2000, we surveyed the bayside beach of South Spit from a vehicle on South Spit Road (which runs along the bay shore) 24 times during daylight ebbing tides January–April; the abundance and distribution of all Brant were mapped on an aerial photo of South Humboldt Bay, and grit-ingestion behavior was noted. To better observe all of South Bay in 2001, in addition to 31 South Spit Road surveys, we surveyed the entire South Bay 33 times during daylight ebbing tides in February and March using a 60× spotting scope from an elevated observation site (Bell Hill in Fig. 1); the abundance and distribution of all Brant were mapped on an aerial photo of South Humboldt Bay, and grit-ingestion behavior was noted. We identified 10 main haul-out sites, and observed grit-ingestion behavior at 6 of these (Fig. 1). We based our analyses of grit selection on the three most used grit-ingestion sites (A, B, and C in Fig. 1) used by 78% of all Brant.

Movement.—To estimate movement probabilities between grit-ingestion sites, we read tarsal bands of all Brant at the three most used grit-ingestion sites (A, B, and C in Fig. 1). Brant were banded at major breeding and molting locations; all ages of individual Black Brant have been marked annually with uniquely coded tarsal bands resulting in ~8% of the total population being banded (Sedinger et al. 1993, Ward et al. 1993, Bollinger and Derksen 1996). On 24 days between January and April 2000, we used a 60× spotting scope on the bay-side shore of South Spit to read the leg bands of Brant ingesting grit at South Spit sandbars during ebbing tides.

We used multi-strata modeling in program

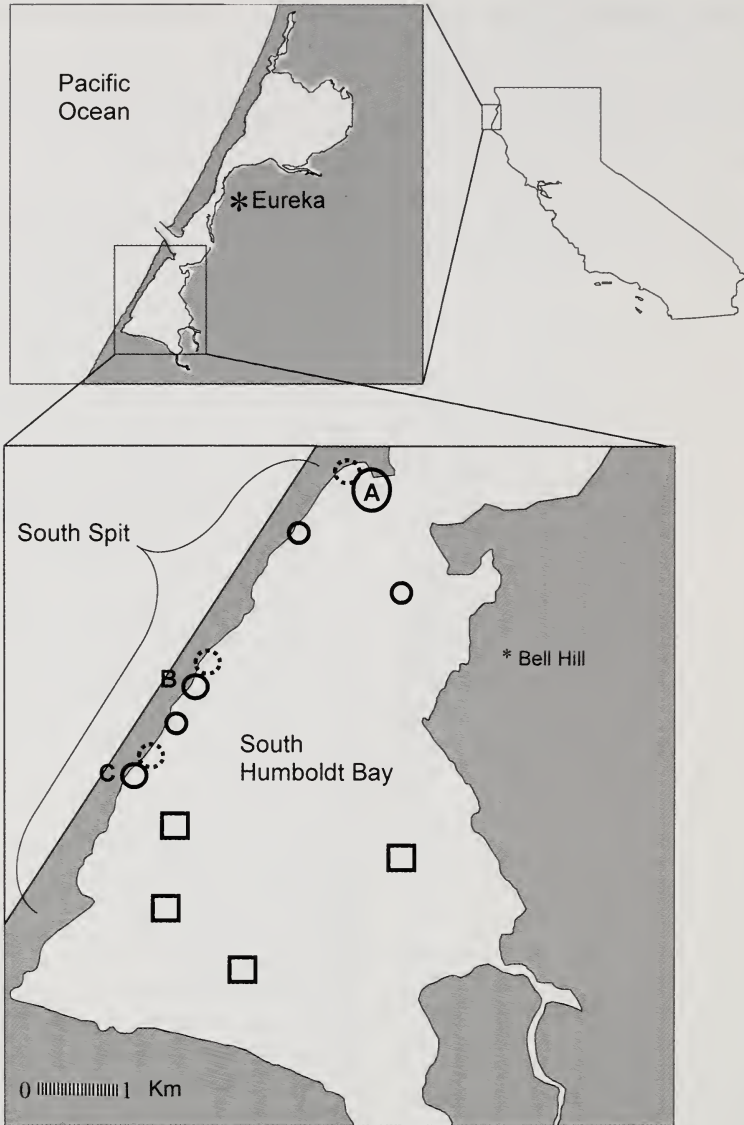


FIG. 1. Study area on South Humboldt Bay, California. Black Brant (*Branta bernicla nigricans*) using grit-ingestion sites were observed from Bell Hill. Grit-ingestion sites are marked with solid-line circles (main sites are labeled A, B, and C). Paired, unused, substrate-sampling sites are indicated by broken-line circles. Roost sites with very fine sediments that were not sampled are indicated with squares.

MARK (White and Burnham 1999) to estimate probabilities of banded Brant moving between grit-ingestion sites. Two strata were defined: North (site A), and South (sites B and C). Sites B and C were combined based on their proximity and to make the number of individuals in each strata more equivalent. Model selection was based in Akaike's information criterion corrected for small sample

size (AIC_c) (Akaike 1974, Burnham and Anderson 1998). All models were run using the logit link function. Goodness-of-fit (GOF) was assessed in a recaptures-only data structure using the bootstrap procedure in program MARK with 100 simulations. The general model for GOF testing was $\{S(\text{site} \times \text{time}) p(\text{site} \times \text{time})\}$, indicating that local study area fidelity (S) and recapture (p) probabilities

varied by site and time. We accepted a general model GOF if its deviance ranked <90 out of the 100 rank-ordered deviances simulated.

Due to weather and tides, leg bands could not be read every day to estimate daily movement probabilities; therefore, we pooled the 24 days of band-reading observations into twelve 7-day intervals. Different pooling intervals were tried with the final selection being the shortest time period that met three criteria: (a) the number of observation periods with no data was 0, (b) the rank of the deviance of the general model was <90th out of 100 ranked bootstrap simulations, and (c) the general multi-strata model $\{S(\text{site} \times \text{time}) p(\text{site} \times \text{time}) \psi(\text{site} \times \text{time})\}$ would converge. Temporal pooling violates the assumptions of instantaneous observations and of a closed population during observations, and can lead to biased parameter estimates (Hargrove and Borland 1994); however, pooling was necessary to estimate movement rates and is commonly practiced (Pradel et al. 1997, Reed et al. 1998).

The *a priori* model set included S , p , and ψ (movement probability) as constants (\cdot), time-dependent (time), and linear trends through time (T), with site effects modeled as (site), (site + time), (site + T), (site \times time), and (site \times T), for a total of eight models for each parameter. We simplified the general model systematically, starting with p , then reducing S and ψ in turn for a total of 24 models tested altogether (Lebreton et al. 1992). The general model $\{S(\text{site} \times \text{time}) p(\text{site} \times \text{time}) \psi(\text{site} \times \text{time})\}$ was reduced by first ranking all eight models for p in the set while holding S and ψ in their general form. After a parsimonious model of p was found, S was reduced by ranking all eight models for S in the set while holding p in its most parsimonious form, and ψ in its general form. Finally, ψ was reduced by ranking all eight models for ψ in the set while holding p and S in their most parsimonious form (Lebreton et al. 1992). The model with the lowest AIC_c value was considered the best or most parsimonious model. Akaike weights (Burnham and Anderson 1998) were computed to denote relative strength of evidence supporting each model.

Often, several models in the final set of top-ranked models appear equally plausible, with ΔAIC_c values near zero and AIC_c weights

comparable to the best model. To account for model selection uncertainty, model averaging was used to create parameter estimates (Burnham and Anderson 1998). Model averaging uses AIC_c weights to calculate the weighted average of each real parameter across all models with AIC_c weights greater than zero.

Grit sampling.—To compare gizzard grit with grit available at grit-ingestion sites, we obtained hunter-donated gizzards to characterize particle-size distributions of gizzard grit. We sampled substrates at grit-ingestion sites and compared those to gizzard grit to determine whether differential selection of particles was occurring. To determine whether calcium content or particle size distribution was the main site-selection factor, we also compared substrate samples from used and unused sites, and between used sites.

During November 2000 and January 2001, hunters donated gizzards, wings, and heads from Brant taken on Humboldt Bay. November gizzards were more likely to be from birds newly arrived from Izembek Lagoon, Alaska, whereas January gizzards were more likely to be from birds either newly arrived from a more southerly stopover site, or from birds overwintering on Humboldt Bay. Extraneous portions of the alimentary canal and fat deposits were removed, gizzards were opened, and all contents washed into a container. Empty gizzard wet weight (g), head length (mm), age (adult or juvenile based on plumage characteristics), and month taken (November or January) were recorded for each bird. Color of the gizzard grit was classified as either predominantly white or black in order to assign its geographic origin. Organic matter was removed from gizzard-grit samples by ignition at 500°C for 4 hr. After removal of organic matter, grit samples were dried at 105°C for 24 hr and filtered through a stack of five sieves (mesh sizes: 0.053, 0.106, 0.25, 0.5, 1.0, and 2.0 mm) for 5 min in a sediment shaker; portions then were weighed. Proportions (by weight) were arcsine transformed for analysis (Zar 1974).

During low tides of 1 and 15 April 2001, we sampled substrate at the three grit-ingestion sites on South Spit with highest mean Brant abundance, and at paired, unused sites within 50 m of used sites. Five samples were collected at each site except at used site A,

TABLE 1. Table of model selection results for local fidelity (S), recapture (p), and movement (ψ) probabilities of 322 Black Brant (*Branta bernicla nigricans*) ingesting grit at two sites on South Humboldt Bay, California, 2000. While the best model (boldface, $\Delta AIC_c = 0$) indicated no difference in movement probability between sites, the two next-best models did include site, and had non-trivial AIC_c weights, thus contributing a substantial site effect (a north-biased movement probability) to the final model-averaged parameter estimates.

Model	AIC_c	ΔAIC_c	AIC_c weights	k	Deviance
{$S(T)$ $p(\text{site} + \text{time})$ $\psi(\cdot)$}^a	687.4	0	0.37	15	241.7
{ $S(T)$ $p(\text{site} + \text{time})$ $\psi(\text{site})$ }	687.7	0.3	0.31	16	239.9
{ $S(T)$ $p(\text{site} + \text{time})$ $\psi(\text{site} \times T)$ }	689.1	1.7	0.16	18	236.9
{ $S(T)$ $p(\text{site} + \text{time})$ $\psi(T)$ }	689.6	2.2	0.12	16	241.7
{ $S(T)$ $p(\text{site} + \text{time})$ $\psi(\text{site} + T)$ }	691.7	4.3	0.04	17	241.6
{ $S(T)$ $p(\text{site} + \text{time})$ $\psi(\text{site} + \text{time})$ }	697.9	10.5	0	26	227.5

^a T = linear temporal trend, site = difference between north and south sites, time = full time dependence, (·) = constant.

where we collected seven samples. Each sample was a volume equivalent to approximately 30 g (dry weight) of sand collected from within 1.5 cm of the surface. Samples were taken at 5-m intervals along a transect that began 10 m down slope from the high tide line, and ran along the ridge of each sandbar toward the water line. In spring 2001, at Izembek Lagoon, Alaska, we also obtained two substrate samples (~30 g each) from the intertidal zone of one of the most heavily used grit-ingestion sites. All substrate samples were dried, filtered, and weighed using the same method described above for analyzing samples of gizzard grit. Our analyses relied upon the assumption that the gizzard grit we collected was ingested from the sites we sampled at Izembek Lagoon and Humboldt Bay. There is no way to confirm the validity of this assumption, but based on the appearance and mineral composition of the grit particles, we are confident they came from the bays in question, if not necessarily from the sampled sites.

To determine calcium content of substrate samples, we used a sample splitter to split entire ~30-g substrate samples, one portion of which was split again to obtain ~7-g samples. Samples were dried at 105° C for 24 hr, cooled in a desiccator, and weighed. Calcium carbonate content was estimated by measuring the volume of gas evolved (corrected for sample weight, temperature, and pressure conditions) when 10 ml of 6 N hydrochloric acid was added to the sample and stirred for 5 min (detailed methods in Machette 1986, modified from Dreimanis 1962). Percent calcium carbonate of each sample was arcsine trans-

formed for analysis (Zar 1974). We used GLM in program NCSS (Hintze 2000) to analyze all gizzard grit and substrate data. Means are reported \pm SE.

RESULTS

Based on 88 surveys, Brant repeatedly hauled out at 10 specific sandbars along South Spit and at fine-sediment bars within the bay (Fig. 1). These sites were discrete and their use by Brant did not change between the 2 years of observation, nor within an observation season. Sites A, B, and C combined were used by 78% of all Brant. Site A, the northernmost grit-ingestion site (Fig. 1), was used by more Brant (site A: mean = 342 birds \pm 73, maximum = 1,580) than the two sites with next-highest abundance estimates (site B: mean = 94 \pm 25, maximum = 250; site C: mean = 105 \pm 53, maximum = 200). Fine-sediment bars around the perimeters of eelgrass beds were also used by Brant hauling out during ebb tides, but grit ingestion at these sites was not documented.

Based on 322 individual encounter histories, the most parsimonious model of ψ (the probability of an individual moving between strata each week) between North (site A) and South (sites B and C) was constant (Table 1), but model-averaged parameters indicated North-biased ψ (North to South: $\psi = 0.123 \pm 0.054$; South to North: $\psi = 0.287 \pm 0.124$). The most parsimonious model of S indicated no difference in local study area fidelity between sites (Table 1). Based on the number of Brant using grit-ingestion sites, and movement probabilities between the sites, we designated the northern site (A) as the primary

TABLE 2. Weight (SE) of gizzards and grit found in the gizzards of Black Brant (*Branta bernicla nigricans*) shot at Humboldt Bay, California, in November 2000 and January 2001.

	November 2000 (n = 31)	January 2001 (n = 14)	P-value ^a
Gizzard wet weight (g)	72.5 (9.9)	102.8 (5.9)	<0.001
Grit-sand weight (g)	6.9 (0.3)	10.0 (0.5)	0.001
Gizzard weight/sand weight	10.5	10.3	
Grit color	Black	White	

^a From *t*-test statistic.

grit-ingestion site, and southern sites (B and C) as secondary grit-ingestion sites.

The activities of Brant observed at the South Spit sandbars were tide-dependent. When water depth over the sandbars was >0.5 m, no Brant were present. When water depth was <0.5 m, but sandbars were still submerged, rafts of up to hundreds of birds would jostle over the still-submerged sandbars, rapidly upending then coming up with mouths overflowing with sand solution. Once the sandbars became exposed as tide waters receded, the few birds still ingesting grit were found at the perimeters of the sandbars or at puddles of water remaining on sandbar surfaces. The three main grit-ingestion sites we focused on were exposed by ebbing tides at nearly the same water level (1.8–1.6 m above MLLW), so no tidally induced sequence of accessibility was present.

Hunters donated 31 gizzards in November and 14 in January. All gizzards collected in November were significantly shrunken due to the birds having recently undertaken their non-stop southward migration. November gizzards contained significantly less grit than those collected from Brant during their "stepping-stone" northward migration in January, although the ratio of gizzard weight to grit weight remained constant between seasons (Table 2). After controlling for month of collection, neither gizzard weight, nor grit-sand weight differed significantly between adult and juvenile birds; thus, ages were pooled for subsequent analyses. Grit samples from birds collected in November contained predominantly black volcanic sand, indicating an origin at Izembek Lagoon, Alaska, the primary fall staging area for Brant (D. H. Ward pers. comm.). Grit samples from birds collected in January contained predominantly white quartz sand—as found at known Brant stopover sites

from Baja California north to Humboldt Bay (DEL pers. obs., D. H. Ward pers. comm.).

We compared particle-size distributions of gizzard grit collected in November with substrate from grit-ingestion sites at Izembek Lagoon (Fig. 2A), and we compared gizzard grit collected in January with substrate collected from grit-ingestion sites at Humboldt Bay (Fig. 2B). In November, gizzard grit was composed mostly of 0.5–1.0 mm particles. In January, gizzard grit was made up of nearly equal proportions of particles 0.25–0.5 and 0.5–1.0 mm in size. Substrate at both Izembek Lagoon and Humboldt Bay was composed of mostly particles 0.25–0.5 mm in size. In both seasons, distributions of gizzard-grit particle size were right-skewed toward larger particles (>0.5 mm) relative to the proportional availability of particle sizes in the substrate (Fig. 2A, B).

We compared particle-size distributions of substrate sand from ingestion sites with sand from unused sites in Humboldt Bay (Fig. 3). We found no differences in particle size distributions between sites where grit was ingested and unused sites. We also compared particle size distributions of sand from primary (site A, north site) and secondary (sites B and C, south sites) ingestion sites (Fig. 4). Relative to the north site, the south sites' distribution was right-skewed, containing larger proportions of particles 0.25–0.5 and 0.5–1.0 mm in size (Fig. 4).

The mean calcium content (proportion calcium carbonate) of substrate from all grit-ingestion sites used by Brant (mean = 0.100 ± 0.042) was not significantly higher ($t = -0.88$, $df = 31$, $P = 0.19$) than at unused sites (mean = 0.088 ± 0.034). However, the calcium content of substrates at the primary ingestion site (site A: mean = 0.137 ± 0.036) was significantly higher ($t = -5.01$, $df = 15$, $P < 0.001$) than at the secondary ingestion

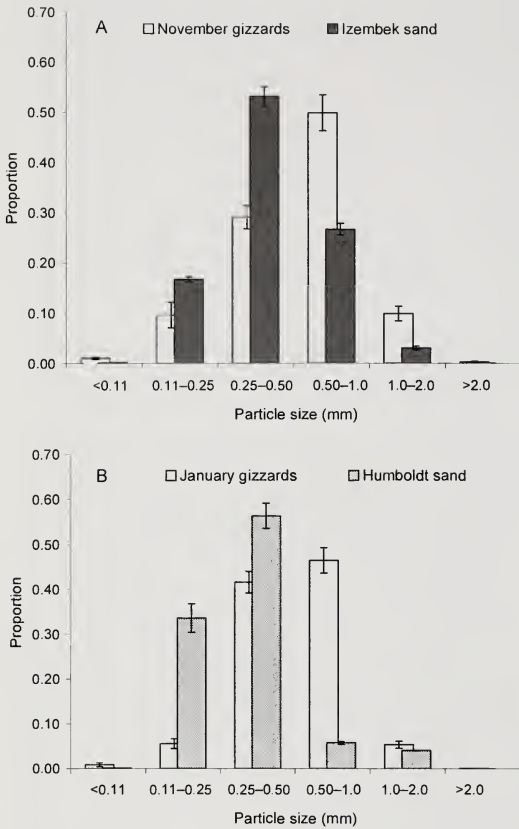


FIG. 2. Particle-size distributions (mean \pm SE) of gizzard grit from Black Brant (*Branta bernicla nigricans*) collected at Humboldt Bay, California in November 2000 compared with substrate from grit-ingestion sites at Izembek Lagoon, Alaska (A); and gizzard grit collected at Humboldt Bay, California in January 2001 compared with substrate from grit-ingestion sites at Humboldt Bay (B).

sites (sites B and C combined: mean = 0.073 \pm 0.018).

DISCUSSION

We documented repeated use by Brant, within and between seasons, of discrete grit-ingestion sites on South Humboldt Bay. Used sites were characterized by differential abundance and constant, low levels of asymmetrical movement by individual Brant between sites. These differences were used to rank the sites as primary and secondary in importance. Only at the level of “within used sites” was there any evidence of differential selection. Our results within used sites indicate that Brant select grit-ingestion sites primarily

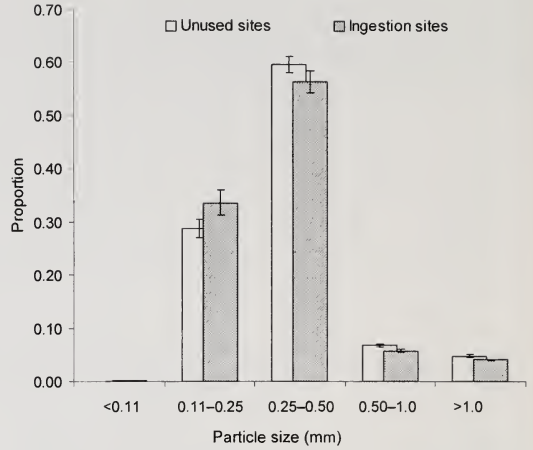


FIG. 3. Particle-size distributions (mean \pm SE) for substrate sand at grit-ingestion sites versus sites not used by Black Brant (*Branta bernicla nigricans*) on South Spit, South Humboldt Bay, California, 2000–2001.

based upon calcium carbonate content of the substrate, and secondarily based upon availability of particle size. These results from field data corroborate the laboratory-based findings of McCann (1939) for Ring-necked Pheasants and Trost (1981) for Mallards.

We interpreted movement toward the preferred site as being calcium driven. That the most preferred grit-ingestion site had higher amounts of calcium carbonate is not surprising considering that eggs are composed of 10–

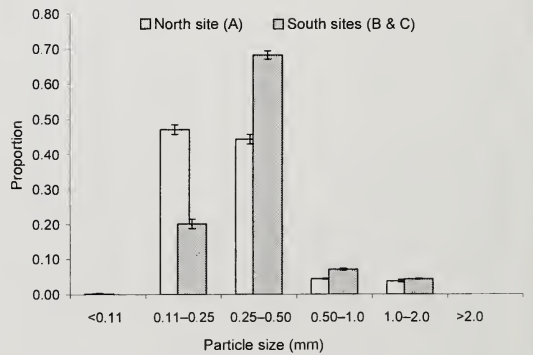


FIG. 4. Particle-size distributions (mean \pm SE) for substrate sand at primary (A) and secondary (B & C) grit-ingestion sites used by Black Brant (*Branta bernicla nigricans*) on South Spit, South Humboldt Bay, California, 2000–2001. Sites were ranked as primary or secondary according to bird abundance and between-site movement probabilities.

15% calcium (Gilbert 1971) and Brant eggshells average 8.2 ± 0.1 g calcium (Ankney 1984). Calcium deficiency has been linked with reduced reproductive success in Great Tits (Graveland and Drent 1997). Graveland and Van Gijzen (1994) found that Great Tits could not obtain sufficient calcium from arthropod and seed food items, but required calcium-rich supplementary material to meet the demands of egg laying. Although Brant are less reliant on endogenous reserves of fat and protein than other arctic-breeding waterfowl due to rich food sources being available near the nest (Ankney 1984), all the calcium requirements of the eggs must be available at the time of laying. For egg formation, birds mobilize calcium from the skeleton and medullary bone (Taylor and Moore 1954, Simkiss 1967), calcium that must be obtained and stored during the nonbreeding season.

Movement toward secondary grit-ingestion sites could have been due to calcium satiation, slightly greater levels of the preferred (larger) grit-particle sizes at secondary sites, displacement by more dominant competitors, and/or avoidance of disturbance. The difference in proportions of particles 0.5–1.0 mm in size between the primary and secondary sites was small, but the difference in handling times required to filter out sufficient quantities of these particles during opportune tidal windows may be enough to explain the attraction to secondary sites where the preferred particle sizes are more abundant. Levels of agonistic behavior were not documented in our study to establish whether competition might drive the movement toward the secondary sites. Brant, however, are sensitive to anthropogenic disturbances (Schmidt 1999), and disturbance may have influenced some of their movements to secondary sites. The primary site is near the main ship channel between South Humboldt Bay docks and both North Humboldt Bay and the Pacific Ocean, while the secondary sites are more remote from human activities.

We found no difference between used and unused sites with respect to particle size or calcium content. No other factors were investigated, thus the factor responsible for specific site use by Black Brant at Humboldt Bay remains unclear. It could have been a function of scale in our experimental design (i.e., se-

lecting paired unused sites at a scale that biased the results toward no difference). A random selection of the comparison sites might have revealed differences. Selection of grit-ingestion sites likely represents a complex interaction of nutritional requirements, social factors, and grit availability.

The right-skewed particle-size distributions of grit found in Brant gizzards versus samples of substrate sand could indicate the ability of Brant to ingest larger sand particles; alternatively, it may reflect differential retention times in the gizzard for different particle sizes. We believe the difference is due to selective ingestion because the only study of gizzard particle retention in waterfowl (using captive Mallards) found no difference in retention rates for particles of different size classes (Trost 1981). Wear (reduction of grit size while resident in the gizzard) could induce only a left-skewed distribution relative to available particle sizes. There is some disagreement over the mechanism waterfowl use to selectively ingest grit particles (Crome 1985, Kooloos et al. 1989, Nudds 1992, Nudds and Wickett 1994, Mateo et al. 2000), but whatever process the birds use, grit-ingestion behavior was much more prevalent when sandbars were still submerged, indicating that Brant prefer to ingest grit when it is in suspension.

Calcium as an essential resource should be more closely examined in grit and food supplies at stopover and breeding sites for all species of migratory birds. Similar studies of newly hatched precocial birds, which need calcium most for skeletal development, would also be instructive. Additionally, calcium requirements for successful reproduction and the ability of various species to store and mobilize skeletal calcium should be determined precisely.

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SHORT-TERM BREEDING BIRD RESPONSE TO TWO HARVEST PRACTICES IN A BOTTOMLAND HARDWOOD FOREST

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ABSTRACT.—Clearcutting is the preferred timber harvest method in bottomland hardwood forests because it is most likely to result in regeneration of preferred species. However, clearcutting generally has negative impacts on forest birds. Patch-retention harvesting may provide similar silvicultural benefits, but its effects on birds are unknown. We surveyed breeding birds in uncut control, clearcut, and patch-retention treatment areas (11–13 ha) for one season prior to harvest and two seasons postharvest in a bottomland hardwood forest in the Lower Coastal Plain of southeastern South Carolina. Bird observations recorded along line transects were analyzed using the software EstimateS to estimate species richness and program Distance to estimate densities. We found greater species richness and bird densities in the patch-retention treatment than in the clearcut in both postharvest seasons. We detected no forest-interior birds in the clearcut after the harvest, but by the second postharvest season in the patch-retention treatment, the density of forest-interior birds had returned to approximately half of its preharvest level. Thus, based on density response, patch-retention harvesting appears to be less detrimental to forest birds than clearcutting. However, additional work is needed to determine whether retained patches influence avian survival and productivity. *Received 30 April 2004, accepted 30 October 2004.*

Bottomland hardwood forests in the southeastern United States serve as critical breeding habitat for numerous avian species, including many considered by Partners in Flight to be of high conservation concern (Hunter et al. 1993, Rich et al. 2004). Historical loss and fragmentation of these forests by conversion to agriculture, development, and other activities, concurrent with possible functional changes in the remaining forests, have likely contributed to the reduction in bird populations (Pashley and Barrow 1993). According to the National Resource Inventory of 1992 (Shepard et al. 1998), the area covered by wooded palustrine wetlands in the South declined by only about 1.5% from 1982 to 1992, a marked reduction in the rate of loss compared with that in preceding decades. Despite this apparent stabilization of forested wetland area, a much higher proportion of woodland Neotropical migrant species was in decline in the eastern United States over the period 1982–1991 than during 1966–1979 (Peterjohn and Sauer 1994). Thus, some aspect of the quality, not just quantity, of the existing bottomland hardwood forest may be a factor in

the decline of birds (Pashley and Barrow 1993). Indeed, much of the extant bottomland hardwood forest is now in streamside management zones and drainages <50 m wide (Kilgo et al. 1998).

Of the approximately 194 million ha of forested land in the United States during 1989, 85 million ha were in the southern U.S. (Wigley and Sweeney 1993). The forest products industry (18.8%) and individual landowners (71.1%) combined held title to nearly 90% of these forested lands (Wigley and Sweeney 1993). Ownership of bottomland hardwoods was apportioned in roughly the same manner, and nearly 20 million ha of non-federally owned, palustrine-forested wetlands were present in the South (Shepard et al. 1998). The primary use of these lands is for timber production (Wigley and Sweeney 1993). If existing bottomland hardwood forests are to remain a viable resource for Neotropical migratory birds, management options that minimize negative effects on breeding birds, but are acceptable to the forest products industry and private landowners, need to be identified and their use encouraged.

From a silvicultural perspective, clearcutting is the favored means of harvesting these forests (Clatterbuck and Meadows 1993, Meadows and Stanturf 1997). Among the reasons for its appeal is that it is the method that best promotes regeneration of shade-intolerant species such as oaks (*Quercus* spp.; Clatter-

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buck and Meadows 1993). The abundance of shrub-successional birds, several of which are of conservation concern (Rich et al. 2004), as well as total bird abundance, can be as great or greater in clearcuts (Hurst and Bourland 1996) and other early successional habitats (Buffington et al. 1997) as in mature bottomland hardwood forest. However, species richness and diversity are highest in mature bottomland hardwoods (Hurst and Bourland 1996, Buffington et al. 1997), and the impacts of clearcutting on most species that prefer mature forest-interior conditions are negative (Hurst and Bourland 1996, Baker and Lacki 1997). Thus, we need alternatives to clearcutting that retain the advantages for forest regeneration but that are less damaging to bird species that inhabit mature forest.

Several studies have been conducted to evaluate the impacts on birds of one such alternative, group-selection harvest. In this method, small groups of mature trees are cleared from a stand at regular spacing intervals (Meadows and Stanturf 1997). Moorman and Gynn (2001) concluded that when adequate mature forest was left unharvested, the abundance of most breeding forest-interior species was not impacted by group-selection harvest. Similarly, Moorman et al. (2002) determined that the productivity of a representative forest-interior species, the Hooded Warbler (*Wilsonia citrina*), was minimally affected. Kilgo et al. (1999) concluded that group-selection harvest gaps benefited many species of migrating forest-interior birds because they used the early successional patches during passage. However, when applied in the strictest sense (gap size no greater than 0.5 ha), this technique usually favors regeneration of stands that are dominated by low-value, shade-tolerant trees because of limitations on light availability (Meadows and Stanturf 1997).

Two-age harvest prescriptions, in which a predetermined quantity of basal area is retained in an even distribution across the site (a modification of the shelterwood method), have also been evaluated (Baker and Lacki 1997, Norton and Hannon 1997, Duguay et al. 2001). In Kentucky, such prescriptions did not alleviate negative effects of clearcutting on the abundance of certain forest-interior birds, but some indices of bird community structure

were higher in harvested areas (Baker and Lacki 1997). In Canadian boreal forest, seven of eight bird species lost from clearcuts were retained at low abundance levels in partial cuts (Norton and Hannon 1997). In hardwood forests of West Virginia, avian abundance and nesting success were comparable for most bird species tested among control areas, two-age harvest, and clearcut treatments 15 years after harvest (Duguay et al. 2001). Both Norton and Hannon (1997) and Duguay et al. (2001) concluded that the two-age method was a viable conservation alternative. However, from a timber management perspective, shelterwood methods can be difficult to implement because of the critical importance of choosing the appropriate establishment cutting intensity (Meadows and Stanturf 1997).

A third alternative, representing a hybrid of group selection and clearcutting methods, is patch-retention harvest, in which residual trees and snags are retained in small patches that mimic or actually represent remnants of the original forest. Patch-retention harvesting is appealing to forest managers, because leaving patches of uncut forest is operationally easier (for equipment such as feller-bunchers) than attempting to retain a high basal area of more evenly distributed trees (Tittler et al. 2001; J. P. Martin, MeadWestvaco Corporation, pers. comm.). Additionally, the incidence of windthrow may be lower for trees in patches compared with isolated residual trees. Reported impacts to forest bird communities have been less severe in patch-retention harvests than in clearcuts within boreal forests of Canada (Schieck et al. 2000, Tittler et al. 2001) and aspen forests in Minnesota (Merrill et al. 1998). However, this method has not been widely tested.

Our objective was to compare the effects on bird species composition of retaining patches of bottomland hardwood forest within a clearcut with performing a traditional clearcut or leaving the forest intact (unharvested control). In particular, we addressed whether the responses of individual species and/or avian habitat-use groups differed between a patch-retention cut and a clearcut area, and whether bird species composition changed in these areas from preharvest to 2 years postharvest. In effect, we sought to determine whether bird species composition of the

patch-retention area more closely resembled that of the unharvested control, particularly with respect to birds that depend on mature forest-interior habitat.

METHODS

The study was conducted on a 350-ha area located in the Lower Coastal Plain of southeastern South Carolina on the floodplain of the fourth-order, blackwater Coosawhatchie River (Burke et al. 2003), a relatively small, anastomosing stream that drains an area of approximately 1,000 km². Topography in the low-relief (≤ 2 m) floodplain is characterized by a network of slightly elevated hummocks and scour channels (Burke et al. 2003). Water tupelo (*Nyssa aquatica*), swamp tupelo (*N. sylvatica* var. *biflora*), sweetgum (*Liquidambar styraciflua*), bald cypress (*Taxodium distichum*), laurel oak (*Quercus laurifolia*), and red maple (*Acer rubrum*) dominate the plant communities of the floodplain (Burke et al. 2000). Where present, the understory (in undisturbed forest) consists of widely scattered patches of *Vaccinium* spp., *Sabal minor*, and *Arundinaria gigantea*; very little under- or midstory structure exists.

Three 11- to 13-ha treatment areas were established in the fall of 1999: an uncut control, a patch-retention area, and a clearcut. This size range approximated an operational harvest. The three treatment areas were arranged linearly, parallel to the direction of water flow. They were approximately equidistant (300–400 m) from the main body of the Coosawhatchie River and were similar with respect to soils, hydrology, and preharvest plant communities (Burke et al. 2000, Eisenbies and Hughes 2000, Murray et al. 2000). A 100-m forested buffer separated the patch-retention from the clearcut area, with a somewhat narrower and more irregular buffer between the uncut control and patch-retention areas. In the patch-retention treatment, three “patches” of two sizes (two 0.20 ha and one 0.61 ha) were left uncut, one each in an area representative of a convex, concave, or flat landform. Thus, 1.01 ha of forest was retained within the 13.1-ha patch-retention treatment area. Using the average basal area for the study site (46 m²/ha; Burke et al. 2003), the residual basal area of the patch-retention treatment was 3.6 m²/ha.

We surveyed breeding birds along line transects (Bibby et al. 2000) for 1 year preharvest (1999) and 2 years postharvest (2000–2001). We arranged transects such that each treatment area was completely covered without duplication of coverage, assuming a 50-m detection zone on each side of the line. We conducted three to four counts each year between 15 May and 11 June. Single-observer surveys began around 06:00 EST and continued until all treatments had been surveyed, usually around 11:00. During each survey, the observer proceeded along the transect, stopping only to record detections. The observer mapped locations of all birds encountered by sight and/or sound and estimated the perpendicular distance (0–50 m, to the nearest 10 m) from the transect line to detected individuals. To account for the potentially confounding effect of time of day, we varied the order in which the treatments were surveyed.

We estimated species richness using the software EstimateS, ver. 6.0b1 (Colwell 1997). Based on detection data, this program provides values for several species-richness estimators. We present the first-order jackknife estimates because they are robust and have performed well in other studies (as cited in Nichols et al. 1998, Hellmann and Fowler 1999). We obtained density estimates using program Distance, ver. 3.5 (Thomas et al. 1998). We used grouped data (10-m intervals) stratified by treatment and year. Although they were not independent, we treated each visit to a given treatment within a season as a “replicate.” Upon determination of the most appropriate model for the detection function (uniform, half-normal, or hazard rate) using likelihood ratio tests, Distance provides an estimate of density and error (Buckland et al. 1993). Because Distance bases each density estimate on a unique detection function, the estimates can be compared among sites with differences in detectability. We tested for annual differences in estimated density within each treatment area by determining whether the 95% confidence intervals overlapped; we accepted as different those confidence intervals that did not overlap (Hodges and Krementz 1996). We compared density estimates for all birds combined, for individual species with at least 25 observations, and for four avian habitat-use groups: forest interior (I), in-

terior-edge (I-E), field-edge (F-E), and edge-shrub (E-S) (Whitcomb et al. 1981).

Logistical constraints prevented us from replicating our treatment units in an experimental manner; harvesting multiple units on the study area was not feasible or desirable for the landowner. We used a before-after, control impact (BACI) design (Johnson 2002), in which we sampled both before and after the harvest treatments on both control and treatment areas. This design was used in an attempt to minimize the effect of variables unrelated to the treatments. Nevertheless, our results must be viewed with caution, since—lacking replication—we do not know whether they would be applicable on other sites.

RESULTS

Prior to the harvest (1999), the estimated species richness of breeding birds was lower in the control area than in the patch-retention area (Fig. 1). However, we could not make statistical comparisons between the estimate from the clearcut area in 1999 with the others, because it had a variance of 0 (the first-order jackknife estimator uses the number of unique species recorded on multiple visits; since we detected two unique species on each visit, the variance of these identical values was 0). Estimated total density did not differ among the three treatment areas prior to harvest (Fig. 1).

Following harvest, total density was similar and species richness actually increased in the uncut control area. However, both measures declined immediately after harvest (2000) in both the clearcut and patch-retention areas (Fig. 1). The decrease was especially large in the clearcut, where estimated species richness declined from 25.0 to 9.3, and estimated density fell from 33.0 to 2.8 pairs/10 ha. In the second postharvest year (2001), density increased in both the clearcut (Fig. 1) and patch-retention (nonsignificantly) areas. Species richness rebounded in the patch-retention area, rising from 15.3 to 25.0, but not in the clearcut. From preharvest to 2 years postharvest in the clearcut, 15 species of the forest-interior or interior-edge groups disappeared, whereas 5 species of these groups disappeared in the patch-retention area (Tables 1 and 2). During the postharvest period, species composition also changed in both treatments. In the clearcut, only 2 of 11 (18%) species de-

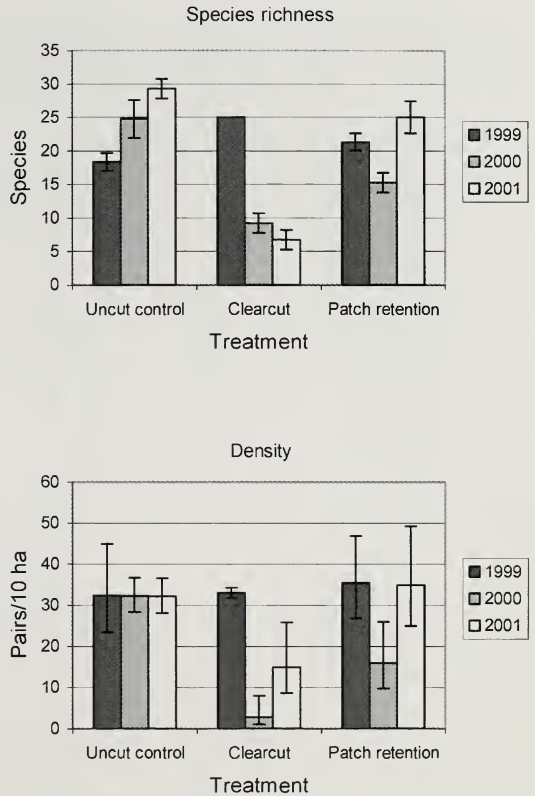


FIG. 1. Species richness and density (mean \pm 95% confidence intervals) for breeding birds in three harvest treatment areas in a bottomland hardwood forest in South Carolina, 1999–2001. No confidence interval is given for species richness in the clearcut area in 1999 because the variance was 0 (see text for explanation).

ected postharvest were recorded in both postharvest seasons (Tables 1 and 2), whereas in the patch-retention area, 11 of the 21 (52%) species detected postharvest were recorded in both seasons.

In the patch-retention area, 35 of 43 (81%) birds observed in 2000 were recorded within retained forest patches, but in 2001, only 37 of 89 (42%) observations occurred in retained forest patches. Although the total number of birds observed in the patch-retention area essentially doubled, the number of birds observed within the retained patches remained about the same.

We estimated densities for 11 species (Table 1). Individual species appeared to respond to the clearcut treatment in different ways. Three of the 11 species had disappeared after

TABLE 1. Densities [pairs/10 ha (95% confidence interval)] of selected bird species in uncut control, clearcut, and patch-retention treatment areas in a bottomland hardwood forest in South Carolina, 1999–2001. Bold-faced entries (within treatment areas) are significantly different from the 1999 value.

Species (no. of observations)	Uncut control			Clearcut			Patch retention		
	1999	2000	2001	1999	2000	2001	1999	2000	2001
Forest-interior species									
Acadian Flycatcher (93) (<i>Empidonax virescens</i>)	4.47 (1.97–10.2)	5.03 (3.54–7.16)	2.80 (1.65–4.75)	4.88 (1.24–19.3)	0	0	3.63 (1.36–9.68)	0	0.18 (0.01–2.57)
Interior-edge species									
Red-bellied Woodpecker (35) (<i>Melanerpes carolinus</i>)	1.99 (1.16–3.40)	1.12 (0.40–3.14)	1.68 (0.86–3.28)	1.44 (0.27–7.53)	0	0	0.97 (0.13–7.39)	0.18 (0.01–2.57)	0.36 (0.03–5.14)
Great Crested Flycatcher (37) (<i>Myiarchus crinitus</i>)	1.24 (0.15–10.5)	0.74 (0.21–2.60)	1.86 (0.99–3.50)	0.86 (0.09–8.66)	0.65 (0.23–1.81)	0	1.45 (0.19–11.1)	1.26 (0.26–6.05)	0.36 (0.07–2.00)
Red-eyed Vireo (127) (<i>Vireo olivaceus</i>)	7.24 (4.72–11.1)	4.66 (3.19–6.82)	4.47 (3.60–5.55)	8.26 (5.34–12.8)	0.22 (0.02–3.05)	0	6.05 (3.84–9.53)	2.38 (1.48–3.83)	0.54 (0.08–3.50)
Carolina Chickadee (43) (<i>Poecile carolinensis</i>)	2.34 (0.48–11.5)	1.49 (0.30–7.46)	1.68 (0.52–5.39)	0.86 (0.02–31.0)	0.43 (0.08–2.37)	0	4.44 (1.47–13.4)	0.54 (0.08–3.50)	1.93 (1.07–3.49)
Tufted Titmouse (50) (<i>Baeolophus bicolor</i>)	1.74 (0.36–8.38)	2.42 (1.17–5.00)	1.49 (0.78–2.84)	2.87 (0.64–12.9)	0.22 (0.02–3.05)	0	1.45 (0.43–4.91)	0.36 (0.07–2.00)	0.54 (0.19–1.53)
Carolina Wren (47) (<i>Thryothorus ludovicianus</i>)	1.24 (0.53–2.91)	1.12 (0.30–4.15)	1.31 (0.56–3.07)	1.15 (0.40–3.31)	0	0.65 (0.10–4.15)	2.42 (1.58–3.72)	0.73 (0.73–0.73)	3.33 (0.95–11.7)
Blue-gray Gnatcatcher (131) (<i>Poliptila caerulea</i>)	7.18 (3.45–15.0)	8.01 (6.29–10.2)	9.09 (7.30–11.3)	4.71 (0.82–26.9)	0.65 (0.23–1.81)	1.29 (0.23–7.12)	8.95 (6.60–12.1)	1.27 (0.81–2.00)	2.36 (1.28–4.35)
Northern Parula (72) (<i>Parula americana</i>)	2.24 (0.45–11.1)	3.17 (2.22–4.53)	2.98 (2.16–4.12)	4.31 (2.62–7.07)	0	0	2.66 (0.51–13.8)	0.18 (0.01–2.57)	2.02 (0.31–13.0)
Common Yellowthroat (42) (<i>Geothlypis trichas</i>)	0	0	0	0	0	7.25 (4.81–11.0)	0	0	7.02 (4.36–11.3)
Edge-shrub species									
Indigo Bunting (27) (<i>Passerina cyanea</i>)	0	0	0	0.29 (0.01–10.3)	0	2.37 (1.37–4.10)	0	0	5.25 (2.21–12.5)

TABLE 2. Number of bird observations in uncut control, clearcut, and patch-retention treatment areas in a bottomland hardwood forest in South Carolina, 1999–2001. Included are all species not analyzed using program Distance (Thomas et al. 1998).

Species	Uncut control			Clearcut			Patch retention		
	1999	2000	2001	1999	2000	2001	1999	2000	2001
Forest-interior species									
Barred Owl (<i>Strix varia</i>)	0	0	1	0	0	0	0	0	0
Pileated Woodpecker (<i>Dryocopus pileatus</i>)	2	1	5	0	0	0	0	0	1
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	0	11	6	1	0	0	2	0	2
Pine Warbler (<i>Dendroica pinus</i>)	0	0	0	2	0	0	1	0	0
American Redstart (<i>Setophaga ruticilla</i>)	0	0	1	0	0	0	0	0	0
Ovenbird (<i>Seiurus aurocapilla</i>)	0	0	1	0	0	0	0	0	0
Kentucky Warbler (<i>Oporornis formosus</i>)	0	0	3	0	0	0	0	0	0
Hooded Warbler (<i>Wilsonia citrina</i>)	0	1	0	0	0	0	0	0	0
Interior-edge species									
Yellow-billed Cuckoo (<i>Coccyzus americanus</i>)	4	0	2	3	0	0	3	0	0
Downy Woodpecker (<i>Picoides pubescens</i>)	3	7	8	2	0	0	0	3	0
Eastern Wood-Pewee (<i>Contopus virens</i>)	0	1	0	0	0	0	0	4	1
White-eyed Vireo (<i>Vireo griseus</i>)	1	2	0	0	1	0	1	0	0
Yellow-throated Vireo (<i>Vireo flavifrons</i>)	3	4	4	4	0	0	0	0	1
Blue Jay (<i>Cyanocitta cristata</i>)	0	0	0	2	0	0	1	0	0
Prothonotary Warbler (<i>Protonotaria citrea</i>)	1	5	2	5	0	0	2	0	0
Summer Tanager (<i>Piranga rubra</i>)	0	2	5	1	0	0	0	2	1
Northern Cardinal (<i>Cardinalis cardinalis</i>)	5	1	1	4	2	3	1	1	4
Edge-shrub species									
Red-headed Woodpecker (<i>Melanerpes erythrocephalus</i>)	0	2	0	0	0	0	1	0	0
Field-edge species									
Killdeer (<i>Charadrius vociferus</i>)	0	0	0	0	0	0	0	2	0
American Crow (<i>Corvus brachyrhynchos</i>)	3	2	2	2	0	0	3	0	1
Yellow-breasted Chat (<i>Icteria virens</i>)	0	0	1	0	0	0	0	0	0
Eastern Towhee (<i>Pipilo erythrophthalmus</i>)	0	0	1	0	0	0	0	0	0
Field Sparrow (<i>Spizella pusilla</i>)	0	0	0	0	0	0	0	0	1
Blue Grosbeak (<i>Passerina caerulea</i>)	0	0	0	0	0	2	0	0	0
Wetland species									
Wood Duck (<i>Aix sponsa</i>)	0	0	0	1	0	0	0	0	0

the first postharvest year, and seven (e.g., Acadian Flycatcher, *Empidonax virescens*; Red-eyed Vireo, *Vireo olivaceus*; and Northern Parula, *Parula americana*; all Neotropical migrants) had disappeared by the second postharvest year. Only two species detected more than once before the harvest, Carolina Wren (*Thryothorus ludovicianus*) and Blue-gray Gnatcatcher (*Polioptila caerulea*), used the clearcut in the second postharvest year. Finally, Common Yellowthroat (*Geothlypis trichas*) and Indigo Bunting (*Passerina cyanea*), which were essentially absent preharvest (only one observation of Indigo Bunting in 1999) and in the first postharvest season, colonized the clearcut in the second postharvest

year and accounted for 70% of the total observations.

In the patch-retention treatment, as in the clearcut, the abundance of most species we analyzed appeared to decline in the first postharvest year, but only Acadian Flycatcher was not observed at all. During the second postharvest season, however, abundance of most species stabilized or rebounded slightly; for 9 of 11 species, densities in 2001 were not significantly less than those in 1999. Common Yellowthroat and Indigo Bunting, absent during the preharvest and the first postharvest seasons, accounted for 40% of the total observations in this treatment during the second postharvest year.

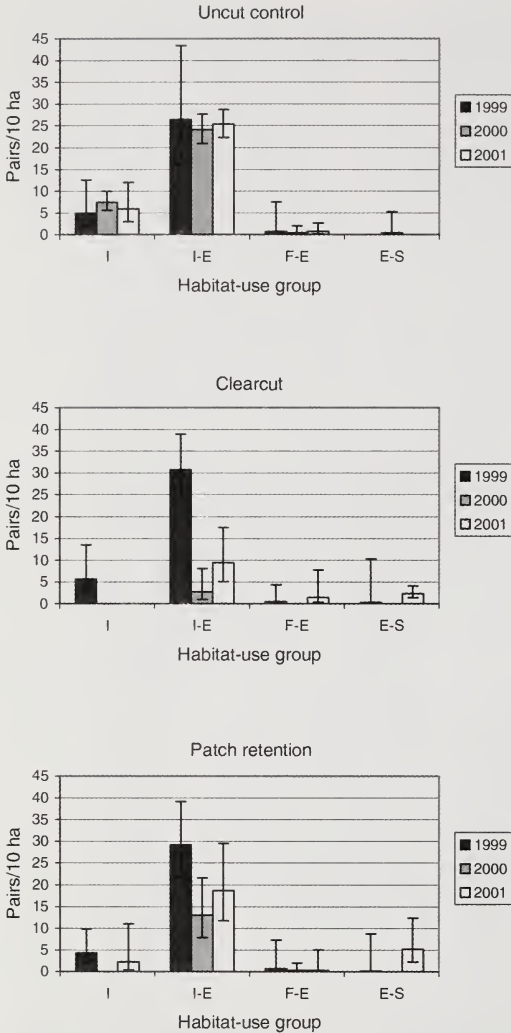


FIG. 2. Densities of avian habitat-use groups (mean \pm 95% confidence intervals) in three harvest treatment areas in a bottomland hardwood forest in South Carolina, 1999–2001. I = Forest Interior, I-E = Interior-Edge, F-E = Field-Edge, and E-S = Edge-Shrub.

Density estimates within each of the four habitat-use groups did not differ over the 3 years in the uncut control area (Fig. 2). However, in both the clearcut and patch-retention areas, the density of the forest-interior group declined in the first postharvest year. In the second postharvest year, density of forest-interior birds rebounded in the patch-retention area, but not in the clearcut. Density of the forest-interior group was also greater in the patch-retention area than in the clearcut in the

second postharvest season. The density of the edge-shrub group increased in both of these treatment areas in the second postharvest year, due primarily to the abundance of Indigo Buntings (Table 1).

DISCUSSION

Retention of patches of forest within an otherwise clearcut area appears to enhance postharvest forest bird diversity compared to that in clearcuts without such patches (Merrill et al. 1998, Schieck et al. 2000). We observed greater species richness and overall bird densities in the patch-retention treatment area than in the clearcut in both 2000 and 2001. A high percentage of the total bird detections in the patch-retention area were recorded inside retained patches. By the second postharvest year, the estimated density of the forest-interior group in the patch-retention area had recovered to approximately half that in the uncut control, whereas in the clearcut, no individuals of this group were detected. These findings corroborate the results of studies from other regions. For example, in aspen forests of northern Minnesota, Merrill et al. (1998) found high bird diversity in 0.54-ha patches within clearcuts that averaged 14.6 ha. Similarly, the overwhelming majority of birds detected in our postharvest patch-retention area (excluding Common Yellowthroat and Indigo Bunting) occurred inside the patches. Merrill et al. (1998) noted that birds using retained patches did not necessarily nest there but used them for foraging, singing, or other activities. In boreal forest of Alberta, Canada, avian community composition in harvested sites was most similar to that of unharvested, old growth sites when retained trees and snags included large trees and were clumped together (Schieck et al. 2000). Such clumps may have resembled the original forest by preserving some of its structure and microclimates (Schieck et al. 2000).

The harvested portions of both the clearcut and patch-retention areas had been colonized by early successional species (e.g., Common Yellowthroat, Indigo Bunting) by the second postharvest year. Their appearance in the second year after harvest was not unexpected, as at least one growing season is required for establishment of early successional grasses and forbs. Moorman and Guynn (2001) also re-

ported these species in small group-selection cuts in bottomland hardwoods during the second postharvest year. Migratory songbirds may discover potential future breeding habitat during the season-ending dispersal phase and return there the following year (Brewer and Harrison 1975, Morton 1992).

We suggest that patch-retention timber harvest may be more desirable than clearcutting when landowners are interested in maintaining songbird habitat, and that its impacts on bird populations warrant further investigation. Patch-retention harvesting offers some of the silvicultural advantages of clearcutting, but maintains elements of the preharvest stand that are apparently attractive to songbirds. Our findings indicate that, to some degree, the residual patches of forest continue to be used by forest birds, while the surrounding clearcut portion provides suitable habitat for edge-shrub and other early successional species.

That the densities of many birds did not differ in the patch-retention area before and after harvest does not necessarily indicate that the habitat quality was similar (Van Horne 1983). Site fidelity among individual birds may explain some use of the patches after harvest (though not the increased use in the second postharvest year), even if the quality of the patches was poor. Whether retained forest patches have negative impacts on avian population dynamics is unclear, as our study did not address this question. Field-forest edges may be ecological traps for birds by concentrating nesting activity but also attracting nest predators (Gates and Gysel 1978). Similarly, the patches may provide perches for Brown-headed Cowbirds (*Molothrus ater*), facilitating parasitism of nearby nests. Thus our retention patches, with their high edge:area ratios, could possibly have functioned as population sinks. However, studies in which the effect of variable tree retention (two-age type harvests) on nesting success has been examined have generally found little or no evidence for such a phenomenon (Tittler and Hannon 2000, Duguay et al. 2001, Stuart-Smith and Hayes 2003), and cowbird parasitism rates in southeastern forests are low (Kilgo and Moorman 2003). Nevertheless, avian productivity in residual forest patches such as those in our patch-retention treatment has yet to be deter-

mined, and this issue should be the focus of future research.

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CORRELATES OF FALL–SPRING MASS DYNAMICS OF NORTHERN BOBWHITES

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ABSTRACT.—We examined the relationship of trends in fall–spring mass of 330 Northern Bobwhites (*Colinus virginianus*) with photoperiod, air temperature, energy requirements, and supplemental feeding in the Texas Panhandle during 2000–2003. Mass of bobwhites increased from September to December, at which point it peaked and then decreased through March. Mean monthly mass was negatively correlated with photoperiod ($r = -0.89$) and temperature ($r = -0.79$) and positively correlated with energy required ($r = 0.79$; estimated using air temperature). From September to March, bobwhites occupying areas where supplemental feed was provided ($n = 246$) were greater in mass ($\bar{x} = 193.4$ g, 95% CL = 191.6–195.1) than bobwhites in areas without supplemental feed ($\bar{x} = 186.5$ g, 95% CL = 184.0–189.0, $n = 84$), but mean monthly mass was different only during November ($\bar{x} = 197.8$ g, 95% CL = 195.3–200.3 for food-supplemented; $\bar{x} = 188.0$ g, 95% CL = 185.0–191.0 for unsupplemented). Abiotic factors, such as photoperiod and temperature, are confounding factors when attempting to explain fall and winter trends of bobwhite mass. Temporal changes in activities (daily foraging, nocturnal roosting) and their energetic costs (e.g., thermoregulation) also complicate issues of trends in mass. Received 12 April 2004, accepted 17 October 2004.

Abiotic factors have a profound influence on a species' distribution and success (e.g., reproductive success; Putman and Wratten 1984). For example, temperatures can limit a species' distribution as a result of the species' energy requirements (e.g., consuming and converting forage at a rate high enough for survival during low temperatures) and thermal tolerances. Similarly, photoperiod affects behavior by limiting the length of activity periods (e.g., time available for foraging). Thermal tolerances, energy requirements, and behavioral activities all seem to have a relationship with body mass.

Bergmann's Rule (Allee et al. 1949:119–120) states that there is a positive relationship between body mass and latitude within a species' geographical distribution, with certain exceptions (e.g., migratory birds). There is considerable evidence that this rule applies to Northern Bobwhites (*Colinus virginianus*; Leopold 1945, Hamilton 1957, Ripley 1960, Robel and Linderman 1966, Guthery 2000:fig. 18a). Seasonal differences in mass of bobwhites also exist (Robinson 1957). Consequently, spatial and temporal effects must be considered when making comparisons of bob-

white mass. Also, avian physiology and behavior combine with environmental factors to influence mass dynamics (Baldwin and Ken-deigh 1938).

Mass has certain thermal consequences that relate to energetics (e.g., thermal inertia and the energetic costs of thermoregulation). Allee et al. (1949:119) noted that mass differences due to latitude are "usually interpreted in relation to heat conservation in the north and to heat radiation in the south." Essentially, greater mass is advantageous in northern latitudes (heat conservation), while the opposite holds in southern latitudes (heat dissipation). Although Allee et al. (1949) were relating mass to latitude, their statement may apply to the thermal advantages of seasonal variations in mass, as well (i.e., increasing mass during winter and decreasing mass during summer).

Case and Robel (1974) speculated that mass of bobwhites may be affected by the duration of activity periods and environmental temperatures. Others have also discussed the relationships between bobwhite mass and photoperiod (Kirkpatrick 1957, Robinson 1957:49–50), season (Hamilton 1957), and supplemental feeding (Robel 1972), but there is no comprehensive work that addresses these issues for bobwhites. Our objectives were to attempt to explain trends of mass in bobwhites during fall and winter relative to photoperiod, temperature, energetics, and supplemental feeding.

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METHODS

This study was conducted in the Tallahone Pasture (802 ha) of the Mesa Vista Ranch (11,330 ha) in the Panhandle of Texas from September to March 2001–2003. The ranch, 27 km north of Pampa, Texas, in Roberts County, has a 200-day growing season and receives an average 52.6 cm of precipitation annually (Odintz 1996). Average maximum and minimum daily temperatures are 34° C in July and -7° C in January, respectively (Odintz 1996). The climate is classified as steppe: winters are dry and typically mesothermal, although occasionally a microthermal winter occurs (Jordan et al. 1984:fig. 2.19). The vegetation is classified as Rolling Plains (Gould 1975:fig. 1); grasses included little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), western wheatgrass (*Elymus smithii*), and switchgrass (*Panicum virgatum*); forbs included annual buckwheat (*Eriogonum annuum*), western ragweed (*Ambrosia psilostachya*), and Texas croton (*Croton texensis*); woody species included sand sagebrush (*Artemisia filifolia*), cottonwood (*Populus deltoides*), sand plum (*Prunus augustifolia*), saltcedar (*Tamarix gallica*), and fragrant sumac (*Rhus aromatica*); other prominent species were plains pricklypear (*Opuntia macrorhiza*) and plains yucca (*Yucca glauca*). The area's major soil type derives from geological depositions of Late Cenozoic High Plains alluvium, featuring dark loamy mollisols (Jordan et al. 1984:37–38).

Tallahone Creek, which bisects the Tallahone Pasture study area, serves as an ecological barrier for bobwhite populations (west and east sides of the creek). Bobwhites rarely crossed from one side to the other (<15 occasions in >9,200 radiolocations during October 2000–July 2003; Guthery et al. 2004) because of dense, decadent stands of switchgrass >300 m wide that apparently inhibited bobwhite movements between feeder treatments.

The two sides of Tallahone creek differed with respect to bobwhite habitat, which consisted of mottes and stands of sand plum and/or fragrant sumac (Puckett 2002). This cover type composed 25.2% of the west side and 11.2% of the east side. Sand sagebrush communities occupied 33.5% of the west and

39.6% of the east side. The balance of habitat types consisted primarily of grass bottomland, riparian, and shallow upland cover.

The Tallahone Pasture had 40 permanent, stationary feeders filled with a mixture of cereal grains (cracked corn, milo, wheat) during October through March each winter. The feed bins (gravity flow) were on pedestals about 1 m above the ground. Feeders were placed along ranch roads (about 100–400 m apart) in mottes of fragrant sumac or sand plum. Supplement was also spread along major ranch roads 2× per week during the same period. To reduce the amount of feed consumed by white-tailed deer (*Odocoileus virginianus*), ranch personnel fitted feeders with external guards during winter 2002–2003.

We used a crossover design (east and west sides of the creek) to determine the effects of food supplementation on the mass of bobwhites. During the winter of 2000–2001, supplemental feed was present on both sides of Tallahone Creek (21 feeders on the west, 17 ha/feeder; 19 on the east, 23 ha/feeder). During the winter of 2001–2002, food supplementation occurred on the east side of the creek only, whereas during the winter of 2002–2003, feeding occurred on the west side only. Thus, we had a pretreatment comparison when supplemental feed was present simultaneously on both sides as well as a crossover of treatments to cancel out possible effects of differences between the east and west sides of Tallahone Creek. To test for effects of supplemental feeding, we grouped mass data into supplemented (winter 2000–2001, both sides; winter 2001–2002, east side; winter 2002–2003, west side) and unsupplemented (winter 2001–2002, west side; winter 2002–2003, east side) birds.

We used live traps to capture bobwhites (Stoddard 1931:442–445, Schemnitz 1994) from September through March 2001–2003. Traps were baited with a milo-corn mixture and checked twice daily (mid-morning and just before dusk) to minimize stress and injury to birds. We leg-banded and radio-marked a subset of captured individuals as part of a larger study of bobwhite ecology. We used night lighting (Labisky 1968) to capture and radio-mark quail that were roosting with pairs or coveys with ≥1 radio-marked individual.

Individuals were classified as juvenile or

adult on the basis of coloration of the primary covert tips, and they were sexed according to throat-patch coloration (Johnsgard 1975:81, 84). Individual birds were placed in a nylon stocking (≤ 2 g) and weighed to the nearest gram using a spring scale (Pesola AG, Baar, Switzerland). Measurements were not corrected for the additional mass of the nylon stocking or food in the crop. Data for juveniles (hatch-year birds) included only individuals that had molted the eighth primary, indicating that they were >150 days old (Rosene 1969: 46). Mass measurements were taken only upon initial capture of each bird. Data were grouped by month.

Although supplement availability started in October of each year, we used September as a pretreatment month from which to start our analyses. We examined photoperiod (i.e., time period from dawn to dusk) and air temperature as possible correlates of fall and winter trends in bobwhite mass. Photoperiod was averaged by month from September through March 2003 using U.S. Naval Observatory (Astronomical Applications Department, Washington, D.C.) data for Pampa, Texas. Ambient air temperature was recorded at 15-min intervals by a stationary weather station (LI-COR Environmental, Lincoln, Nebraska) about 3.2 km from the study area and averaged by month during September 2000–March 2001 and September 2001–March 2002. We did not have air temperature data for September 2002–March 2003, but we felt that the fall and winter 2000–2002 dataset was adequate for calculating average monthly temperatures. Using the monthly temperature averages, we indexed energy requirements (Y ; kJ/day) of bobwhites during winter (w_a) using Guthery's (2002:12–13) modifications of Case and Robel's (1974) equation:

$$Y_{wa} = 205.1 - 3.52T,$$

where T = ambient temperature ($^{\circ}\text{C}$). This equation does not specifically include mass, but rather estimates energy needs for the range of mass (200–220 g) from which it was developed (Case and Robel 1974). We used the Pearson product-moment correlation coefficient (r) to quantify relationships between the dependent variable (mass) and each independent variable of interest (photoperiod, temperature, and energy requirements). We per-

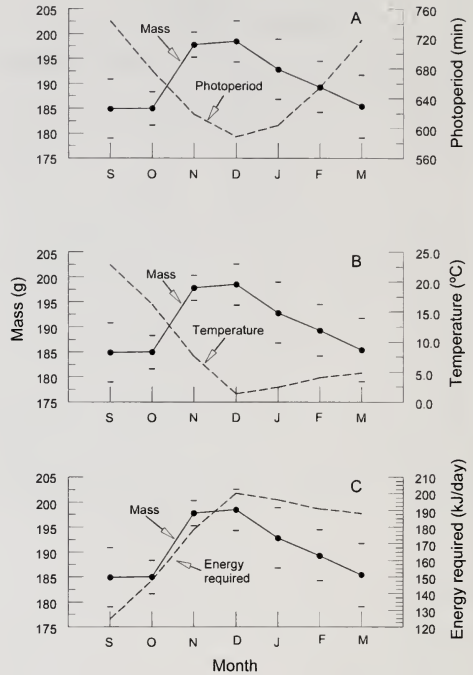


FIG. 1. Relationship of mass of Northern Bobwhites in areas with supplemental feed ($n = 246$), Mesa Vista Ranch, Roberts County, Texas, September–March 2000–2003, with (A) mean monthly photoperiod at the study area, (B) mean monthly ambient air temperature recorded each 15 min by a stationary weather station on the study area, and (C) mean monthly energy requirements calculated from ambient air temperature. Dash symbols represent 95% confidence limits on mass.

formed statistical analyses using SYSTAT 10 (SPSS, Inc. 2000) and ProStat (Poly Software International 2003) at the level $\alpha = 0.05$. Unless noted otherwise, we used t values to calculate confidence limits.

RESULTS

We captured and recorded data from 330 bobwhites >150 days old. To determine trends in mass, we used only the mass data for food-supplemented bobwhites due to the larger sample size ($n = 246$ for food-supplemented, $n = 84$ for unsupplemented). Bobwhites in the study area showed distinct trends in mass during September–March (Fig. 1). Mean mass increased from September to December, when it peaked, and then declined through March.

Mass of food-supplemented bobwhites

TABLE 1. Mean mass (g) of Northern Bobwhites by sex-age class on areas with and without supplemental feed, Tallahone Pasture, Mesa Vista Ranch, Roberts County, Texas, September–March 2000–2003.

Treatment Sex-age class ^a	<i>n</i>	\bar{x}	SE	Range
Food-supplemented				
Female-juvenile	59	192.1	2.2	153–237
Female-adult	52	194.3	1.9	164–222
Male-juvenile	69	191.9	1.5	161–217
Male-adult	66	195.2	1.6	172–222
Pooled	246	193.4	0.9	153–237
Unsupplemented				
Female-juvenile	23	184.8	2.3	166–204
Female-adult	13	185.6	3.3	170–210
Male-juvenile	22	185.1	2.2	160–208
Male-adult	26	189.8	2.4	155–215
Pooled	84	186.5	1.2	155–215

^a Juveniles were defined as individuals that had molted the eighth primary, meaning they were >150 days old.

showed a negative relationship with mean monthly photoperiod ($r = -0.89$; Fig. 1A). Mean monthly photoperiod was lowest (588.3 min) and mass highest ($\bar{x} = 198.3$ g) during December. Mean monthly temperature was also negatively correlated with mass ($r = -0.79$) and was lowest ($\bar{x} = 1.4^\circ$ C) during December (Fig. 1B). Energy needs estimated on the basis of ambient temperature were positively correlated with mass ($r = 0.79$; Fig. 1C). As mean monthly temperature increased after December, energy needs decreased. Estimated energy requirements ranged from 124.7 kJ/day in September to 200.2 kJ/day in December, an increase of 61%. Mean mass of food-supplemented bobwhites from September ($\bar{x} = 184.9$ g) to December ($\bar{x} = 198.5$ g) increased about 14 g, or >7%.

Mean mass was similar among sex-age classes within treatments (food-supplemented, unsupplemented; Table 1), but differed between treatments. From September to March, food-supplemented bobwhites were greater in mass ($\bar{x} = 193.4$ g; 95% CL = 191.6–195.1; $n = 246$) than unsupplemented birds ($\bar{x} = 186.5$ g; 95% CL = 184.0–189.0; $n = 84$). The proportion of food-supplemented (0.52 ± 0.04 SE) and unsupplemented (0.54 ± 0.07) juveniles was similar and therefore did not confound our results. Monthly mean mass differed only in November, when food-supple-

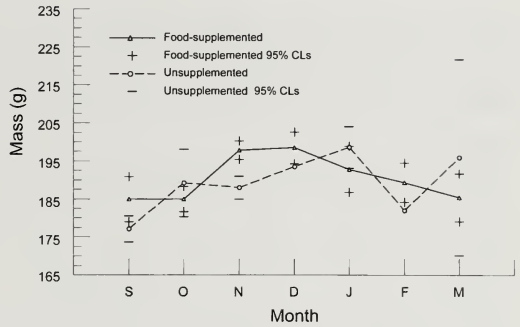


FIG. 2. Relationship between mass of Northern Bobwhites in areas with ($n = 246$) and without supplemental feed ($n = 84$), Mesa Vista Ranch, Roberts County, Texas, September–March 2000–2003. Confidence intervals are not shown for unsupplemented quail in December ($n = 2$) or February ($n = 1$) due to low sample sizes.

mented quail averaged almost 10 g greater mass than unsupplemented quail (Fig. 2).

DISCUSSION

Maximum body mass of quail is expected during winter (Rosene 1969, Case and Robel 1974). This is supported by Robel (1972), who found that bobwhite mass peaked during midwinter, although Roseberry and Klimstra (1971) found that female mass was greater in summer than in winter. Increased winter mass of bobwhites was also observed by Hamilton (1957), Robinson (1957:fig. 11), Robel and Linderman (1966), and Gore et al. (1970), although Hamilton's (1957:table 1) sample sizes were low (e.g., $n = 6$ for December). In other species, particularly passerines, maximum mass also occurs during winter (Baldwin and Kendeigh 1938). Our results generally followed these patterns of increased mass in winter. Also similar to our findings were those of Roseberry and Klimstra (1971:fig. 2; 1984: 109), who found no difference in male and female mass of bobwhites outside the breeding season.

When considering annual mass of bobwhites, Roseberry and Klimstra (1971:fig. 2) found that males had one episode of minimal mass (June) while females had two episodes (March and September). Reproductive activities decrease with the approach of fall, which might explain the increase in mass at that time (i.e., more time budgeted for foraging activities). As winter proceeds, forage availability

decreases, especially with increasing snow cover. This, coupled with the initiation of reproductive activities, may contribute to the general decline in mass of bobwhites after midwinter.

Daily fluctuations in mass also need to be considered. From dusk to dawn, California Quail (*Callipepla californica*) may lose almost 10% of their body mass (Sumner 1935), while bobwhites may lose 5% (Stewart 1937). Since southern bobwhites have about 10% body fat (Dabney and Dimmick 1977, Koerth and Guthery 1987), a 200-g bird could lose 10 g in one night. Warren et al. (1984) found that body fat increases with latitude from south Texas to Kansas. At similar winter temperatures, larger quail in Kansas could conceivably lose less mass than quail in south Texas because of their greater thermal inertia. Although time of capture was not recorded for our bobwhites, traps were generally checked early in the morning and late in the afternoon. Quail caught late in the day may have been at their 24-hr maximum mass (Baldwin and Kendeigh 1938:429).

Decreased photoperiods are associated with increased roosting time. Roosting formations (i.e., roosting disks) become thermally advantageous as temperatures drop below 5°C (Case 1973). Decreasing heat lost to the environment through roost disks obviously decreases energy requirements. Since thermoregulation is the highest energetic cost of bobwhites (Guthery 2002:14), roost disks may provide a substantial energetic advantage. Using thermal radiotransmitters, Guthery et al. (2005) found that when ambient temperatures are <16.2°C, roosting bobwhites could experience temperatures effectively warmer than ambient air temperatures. This might be attributable to roosting disks since winter roost microclimates may hold no energetic advantage (Hiller and Guthery 2005). However, other bird species, primarily passerines that do not form roost disks, also exhibit an inverse relationship between winter mass and temperature (Baldwin and Kendeigh 1938).

In a laboratory experiment, Kirkpatrick (1957) observed increases in mass with decreasing light periods. He also documented nocturnal feeding by confined quail. Our results paralleled those of Kirkpatrick (1957), but within the published literature we found

no evidence of nocturnal feeding by quail in a field setting. Furthermore, within our study area, Hiller and Guthery (2005) observed only roosting at night.

The benefits of greater mass among food-supplemented quail were not obvious. Similar to what we observed, Robel (1972) found that Bobwhites near food plots (<600 m) weighed an average of 9.0 g more than bobwhites far (>900 m) from plots during winter months. Food-supplemented quail also had more body fat (Robel 1969, Robel et al. 1974). However, Guthery et al. (2004) found that, within our study area, supplemental feeding had no effect on survival or cause-specific mortality, but it did concentrate quail near feeders (i.e., decreased home ranges).

Many factors need to be considered when speculating on seasonal variations in body mass. We acknowledge that our analyses present just a few of the potential causes of seasonal mass variation in bobwhites; however, environmental factors (e.g., photoperiod, temperature) may confound attempts to explain fall and winter trends of bobwhite mass. The causal effects of these variables will have to be determined through controlled experimentation.

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A STATISTICAL ANALYSIS OF FACTORS ASSOCIATED WITH HISTORICAL EXTINCTION AND CURRENT ENDANGERMENT OF NON-PASSERINE BIRDS

AUSTIN L. HUGHES¹

ABSTRACT.—Data on historical extinction and current endangerment in non-passerine birds were used to assess associations between vulnerability to human impacts and genus size, range size, and insular endemism. Consistent with the results of previous studies, historical extinction was more frequent in species from monotypic genera, even when other factors were controlled for statistically. By contrast, current endangerment showed no such pattern when other factors were controlled for. Both historical extinction and current endangerment were more frequent in species with restricted ranges and for insular species. Moreover, insular species with restricted ranges were especially vulnerable to current endangerment. Changes between the patterns of historical extinction and current endangerment are likely due to changes in the nature of human impacts over the past 500 years, especially the recent trend toward wholesale habitat destruction. *Received 27 August 2003, accepted 20 September 2004.*

At the present time, the earth's biota is facing an anthropogenic, mass extinction event, unique in the history of our planet (Diamond 1989). It is difficult to predict the ultimate impact of this extinction event, but an analysis of the patterns of recent extinction and current endangerment may enable us to determine trends that will suggest strategies for minimizing the damage (Pimm et al. 1988, Smith et al. 1993, Bibby 1995, Gaston and Blackburn 1997, McKinney and Lockwood 1999, Balmford et al. 2003). Nee and May (1997) showed that a pattern of random extinctions across a phylogeny will conserve nearly as much of the evolutionary history represented by the species in that phylogeny as a strategy explicitly designed to preserve as much of that evolutionary history as possible. This finding may provide hope that the loss of genetic information will be relatively minor.

On the other hand, numerous studies of patterns of historical extinction and recent endangerment in birds and mammals have shown that human impacts on these taxa are far from random, relative to phylogeny (Russell et al. 1998, Hughes 1999, Purvis et al. 2000, von Euler 2001). Those studies have revealed that both historical extinction and recent endangerment have disproportionately affected genera that contain few species, particularly monotypic genera (Russell et al. 1998,

Hughes 1999, Purvis et al. 2000). Assuming that taxonomic classifications at least approximately reflect genetic relationships, such a pattern may suggest a disproportionate human impact on species without close relatives or with few close relatives.

The results of these studies, however, did not clarify the mechanisms behind the apparent tendency of human activities to have greater impacts on species with few or no close relatives. It is possible that some other variable is correlated with scarcity of close relatives. For example, it is well known that human impact has been particularly severe on insular species of birds and certain other groups of organisms (Cronk 1997). Because many insular species have evolved in relative isolation and are thus often assigned to monotypic or species-poor genera, the observed effect may in fact reflect nothing more than the overall vulnerability of insular species.

Russell et al. (1998) and Hughes (1999) compared patterns of historical extinction (since European expansion, beginning in the 15th century) with current patterns of endangerment in order to assess changes in the pattern of human impacts. One of the most striking changes was found in non-passerine birds (Hughes 1999). In both non-passerine and passerine birds, the proportion of historical extinctions was found to be significantly greater in monotypic genera than in polytypic genera. Similarly, in passerines, the proportion of current endangerment was found to be higher in monotypic than in polytypic genera.

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However, in non-passerines, where proportions of both historical extinction and current endangerment were found to be substantially higher than in passerines, there was no difference between monotypic and polytypic genera with respect to rate of current endangerment (Hughes 1999). These results suggest that the nature of human impacts on non-passerine bird species recently changed—from differential impacts on species without close relatives to “across-the-board” impacts.

Here, I analyze data on proportions of historical extinction and current endangerment in non-passerine birds to assess the factors underlying observed patterns. First, I assess the contribution of insularity, restricted range, and genus size to extinction and endangerment, testing for independent effects of each of these factors while controlling statistically for the other factors. Second, I compare the incidence of historical extinction and current endangerment to test the hypothesis that there has been a recent fundamental change in the nature of human impacts on the survival of non-passerine bird species.

METHODS

Analyses were based on data for 3,966 species of non-passerine birds. Species and higher-level taxonomies were based on those recognized by Sibley and Monroe (1990, 1993), including more recently described species recognized by Collar et al. (1994) and Stattersfield et al. (1998). The number of species included in the analysis differs from that in Hughes (1999) because of the addition of three species recognized by Collar et al. (1994) and Stattersfield et al. (1998). Historical extinction was defined as extinction occurring since European expansion (15th century until present). Species were classified as extinct following Sibley and Monroe (1990, 1993), although I also considered the California Condor (*Gymnogyps californianus*; extinct in the wild) as extinct on the grounds that my study emphasizes impacts on natural populations. Any species classified as vulnerable, endangered, or critical by Collar et al. (1994) was classified as currently endangered. Species were classified as insular if their life cycle includes no continental phase. Thus, species whose life cycle involves migration between an island and a continent were not classified

as insular; pelagic feeders breeding exclusively on islands were classified as insular.

I defined restricted-range landbirds as those whose total global breeding range since 1800 was estimated by Stattersfield et al. (1998) to be $\leq 50,000$ km²; however, any species whose current range is $\leq 50,000$ km², but was $> 50,000$ km² at any point since 1800 (Stattersfield et al. 1998), was not counted as a restricted-range species. For a given species, the range size was defined as the area contained within an imaginary boundary (or boundaries, in the case of discontinuous ranges) encompassing all known or inferred sites of occurrence (Stattersfield et al. 1998).

I analyzed data in the form of two $2 \times 2 \times 2 \times 2$ contingency tables. In the first of these tables, all species, whether extant or extinct, were included. I classified species according to four variables: genus size (monotypic, polytypic), insularity (insular, continental), range size (restricted range, non-restricted range), and historical extinction (extinct, non-extinct). The second contingency table included only extant species, which were classified according to four variables: genus size (monotypic, polytypic), insularity (insular, continental), range size (restricted range, non-restricted range), and current endangerment (endangered, non-endangered). Using log-linear models (Everitt 1977), I tested for partial association between extinction and each of the other three variables while statistically controlling for the other two variables. Similarly, in the data set of extant species, I tested for partial association between endangerment and each of the other three variables, statistically controlling for the other two variables. Similar analyses were applied separately to eight families of non-passerine birds (Anatidae, Phasianidae, Rallidae, Columbidae, Psittacidae, Strigidae, Trochilidae, and Picidae). These families were chosen because each included a substantial number of species (≥ 143 species), one or more endangered species, and one or more extinct species.

RESULTS

The proportions of non-endangered, endangered, and extinct species appeared similar in polytypic and monotypic genera (Fig. 1). The major difference was a higher proportion of extinct species among monotypic (2.4%) than

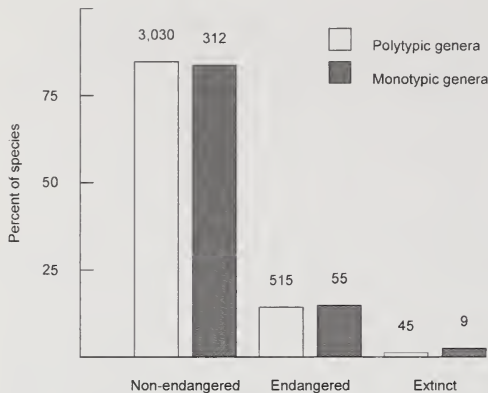


FIG. 1. Percentages of non-passerine species belonging to polytypic and monotypic genera classified as non-endangered, endangered, and extinct. Numbers of species are given above each bar.

among polytypic (1.3%) genera. The partial test of association between genus size and historical extinction was highly significant ($P = 0.006$; all non-passerines; Table 1). However, there was no significant association between genus size and current endangerment (Table 2).

In monotypic but not in polytypic genera, the proportion of extinction was higher in insular than in continental species (Fig. 2). And in both monotypic and polytypic genera, the proportion of endangerment was higher in insular than in continental species (Fig. 2). Log-linear analyses showed a highly significant partial association (all non-passerines; $P < 0.001$) between insularity and both extinction (Table 1) and endangerment (Table 2). Simi-

larly, the proportions of both extinction and endangerment in both polytypic and monotypic genera were higher in restricted-range species than in other species (Fig. 3). Again, log-linear analyses showed a highly significant association between range size and extinction ($P < 0.001$; Table 1) and between range size and endangerment ($P < 0.001$; Table 2).

In log-linear analyses examining all non-passerines for associations with historical extinction, there were no significant ($P < 0.05$) two-way interactions between any pair of variables (Table 1). By contrast, the analysis of current endangerment revealed a highly significant interaction between insularity and range size (Table 2; Fig. 4). Among endangered continental species, non-restricted range species (141 of 287 or 49.8%) and restricted-range species (146 of 287 or 50.2%) accounted for nearly equal percentages of species (Fig. 4). Among endangered insular species, however, the proportion of restricted-range species (195 of 283 or 68.9%) was more than twice that of non-restricted range species (88 of 283 or 31.1%; Fig. 4).

None of the individual families showed a significant partial association between extinction and range size (Table 1). In Psittacidae, there were significant partial associations between extinction and both genus size and insularity (Table 1). In Anatidae and Columbidae, there was a significant partial association between extinction and genus size but not between extinction and insularity (Table 1). On the other hand, in Phasianidae, Rallidae, Trochilidae, and Picidae, there was a significant

TABLE 1. Significance levels for tests of partial association between historical extinction and genus size, insularity, and range size in eight families of non-passerine birds and in all non-passerines.^a

Family	Number of species	Genus size	Insularity	Range size	Genus size × insularity ^b	Genus size × range size ^b	Insularity × range size ^b
Anatidae	148	0.044	NS ^c	NS	NS	NS	NS
Phasianidae	177	NS	0.017	NS	NS	NS	NS
Rallidae	143	NS	0.008	NS	NS	NS	NS
Columbidae	313	0.008	NS	NS	NS	NS	NS
Psittacidae	360	0.008	0.028	NS	NS	NS	NS
Strigidae	143	NS	NS	NS	NS	NS	NS
Trochilidae	324	NS	0.003	NS	NS	NS	NS
Picidae	216	NS	0.017	NS	NS	NS	NS
All non-passerines	3,966	0.006	<0.001	<0.001	NS	NS	NS

^a Entries are P -values for tests of partial association based on log-linear models.

^b Two-way interactions.

^c NS = not significant ($P > 0.05$).

TABLE 2. Significance levels for tests of partial association between current endangerment and genus size, insularity, and range size in eight families of non-passerine birds and in all non-passerines.^a

Family	Number of species	Genus size	Insularity	Range size	Genus size × insularity ^b	Genus size × range size ^b	Insularity × range size ^b
Anatidae	146	NS ^c	0.009	0.035	NS	NS	NS
Phasianidae	176	NS	0.025	<0.001	NS	NS	<0.001
Rallidae	130	NS	NS	<0.001	NS	NS	NS
Columbidae	307	NS	NS	<0.001	NS	NS	NS
Psittacidae	347	NS	NS	<0.001	NS	NS	NS
Strigidae	141	NS	NS	<0.001	NS	NS	NS
Trochilidae	323	NS	NS	<0.001	NS	NS	NS
Picidae	214	NS	NS	NS	NS	NS	NS
All non-passerines	3,912	NS	<0.001	<0.001	NS	NS	<0.001

^a Entries are *P*-values for tests of partial association based on log-linear models.

^b Two-way interactions.

^c NS = not significant (*P* > 0.05).

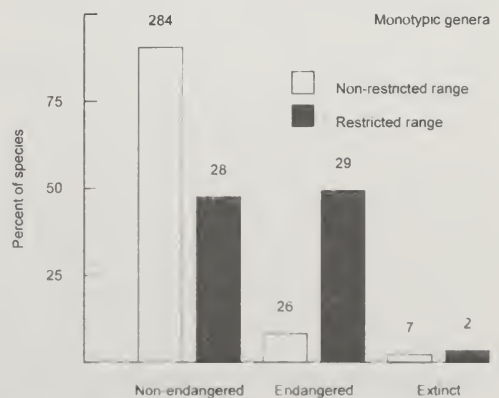
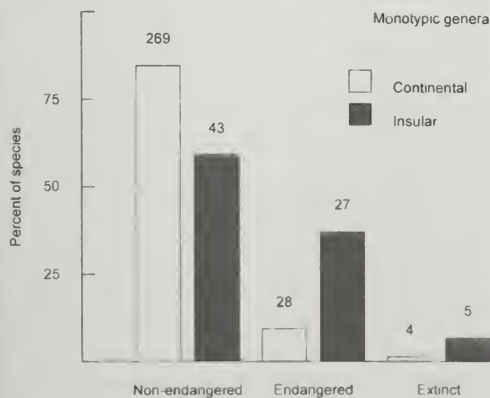
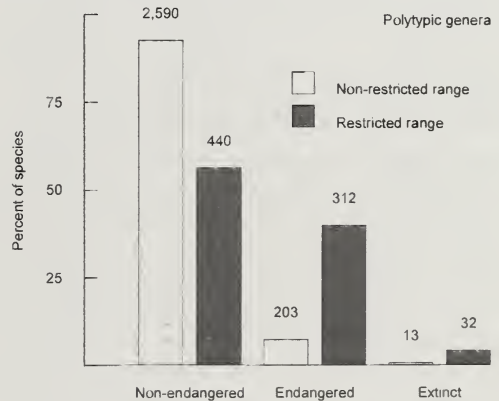
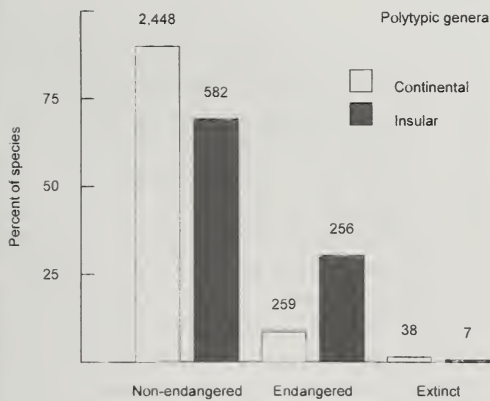


FIG. 2. Percentages of continental and insular non-passerine species classified as non-endangered, endangered, and extinct. Numbers of species are given above each bar.

FIG. 3. Percentages of non-restricted range and restricted-range non-passerine species classified as non-endangered, endangered, and extinct. Numbers of species are given above each bar.

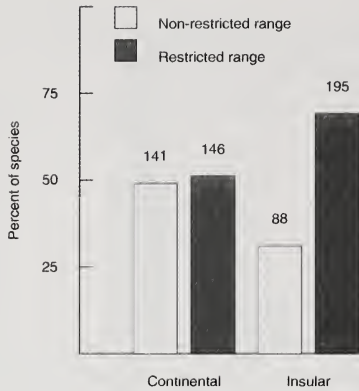


FIG. 4. Percentages of non-restricted range and restricted-range endangered, non-passerine species classified as continental or insular. Numbers of species are given above each bar.

partial association between extinction and insularity but not between extinction and genus size (Table 1). In the analysis of extinction, none of the eight families showed any significant two-way interactions (Table 1).

None of the eight families showed a significant partial association between endangerment and genus size (Table 2). Only Anatidae and Phasianidae showed significant partial associations between endangerment and insularity, whereas all families except Picidae showed significant partial associations between endangerment and range size (Table 2). There was a significant interaction between insularity and range size only in Phasianidae (Table 2). Picidae was unique in showing no significant partial associations with endangerment or two-way interactions (Table 2).

Several authors have noted that the analysis of factors affecting extinction and endangerment may be improved by taking into account autocorrelation between phylogenetically close species (Lockwood et al. 2002, Cassey et al. 2004). In the absence of a phylogeny, Cassey et al. (2004) based autocorrelations on taxonomic categories. To test for effects of taxonomic category, I combined the data from the eight families listed in Tables 1 and 2 and included family as an additional category in the log-linear analysis. None of the effects listed in Tables 1 and 2 showed a significant partial interaction with family, implying that differences among families were not a significant factor in the results reported here.

DISCUSSION

With respect to non-passerine birds, the results reported here are consistent with earlier results (Hughes 1999)—showing both a significantly higher proportion of historical extinctions in monotypic genera and no difference between proportions of current endangerment in monotypic and polytypic genera. Furthermore, these patterns hold true even when the effects of insularity and range size are controlled for statistically. The results support the hypothesis that historic extinction has disproportionately affected non-passerine bird species belonging to monotypic genera regardless of insularity and range size (Table 1). On the other hand, there was no significant association between current endangerment and genus size when the effects of insularity and range size were controlled for (Table 2).

One reason for this difference may be that the most vulnerable non-passerines belonging to monotypic genera have already been driven to extinction (Hughes 1999). The situation is quite different among passerines; the proportion of historical extinctions is considerably lower than that of non-passerines, and currently endangered passerines include a significantly higher proportion of species belonging to monotypic genera than do non-endangered passerines (Hughes 1999). An additional factor may be that historical extinctions of non-passerine species in monotypic genera have included some species with unusual characteristics. For example, extinct non-passerines from monotypic genera include four continental species with very broad ranges: Pink-headed Duck (*Rhodonessa caryophyllacea*), Passenger Pigeon (*Ectopistes migratorius*), Carolina Parakeet (*Conuropsis carolinensis*), and California Condor. These species represent 44% (4 of 9) of all extinct species from monotypic genera. By contrast, only 27.3% (15 of 55) of currently endangered species from monotypic genera are continental species with non-restricted ranges. Thus, one major change has been the loss of a set of geographically widespread but uniquely vulnerable continental species. In the absence of these species, range size and insular endemism have become increasingly important factors in predicting vulnerability.

In contrast to the results for genus size, both

historical extinction and current endangerment were significantly associated with both range size and insularity, even when other variables were controlled for statistically (Tables 1 and 2). The association with range size is not unexpected, since range size is a factor that goes into the assessment of endangered status (Collar et al. 1994). However, the estimates of range size used here were based on historical ranges; thus, some species with currently limited ranges were not scored as "restricted-range" species (Stattersfield et al. 1998). An association between insularity and both extinction and endangerment was hypothesized by Russell et al. (1998) and Hughes (1999), and the present results support this hypothesis.

Nonetheless, there was a striking difference between the results for historical extinction and those for current endangerment when the effect of range size was examined separately for different families. In the case of historical extinction, separate examination of each of eight non-passerine families showed no significant effects of range size (Table 1). By contrast, seven of eight families showed a significant partial association between range size and current endangerment, and in six of these families the association was highly significant (Table 2). These results suggest that non-passerine species with restricted ranges are becoming increasingly vulnerable to human impacts, independent of other factors and in a similar manner across taxonomic categories.

There was a significant interaction between range size and insularity for currently endangered species but not for extinct species (Tables 1 and 2). This interaction is explained by the much higher proportion of restricted-range species that are insular compared with the proportion of restricted-range species that are continental (Fig. 4). This in turn implies that insular species are now doubly vulnerable—by virtue of both their insular distribution and their range size. The absence of such a pattern in the data on historical extinction suggests that this is a new phenomenon, resulting from recent changes in the nature of human impacts. It seems likely that these changes include a trend toward wholesale habitat destruction (Owens and Bennett 2000), to which restricted-range species—especially those on islands—are especially vulnerable.

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FIRST RECORD OF COOPERATIVE BREEDING IN A *THRYOTHORUS* WREN

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ABSTRACT.—Although offspring delay dispersal past the age of independence in many *Thryothorus* species, cooperative breeding has not been recorded in this genus. Here, I present the first observation of cooperative breeding in a *Thryothorus* wren (Buff-breasted Wren, *T. leucotis*). Of 41 offspring that delayed dispersal past the age of independence, 4 individuals stayed on their natal territory until their parent's next breeding attempt, indicating a low potential for cooperative breeding. Of these four individuals, one male provisioned 11- to 15-day-old nestlings and one female approached her parents' nest but was repeatedly driven away from it by her father. The retained female was apparently tolerated when in the vicinity of fledglings, but feeding was never positively confirmed. Received 10 May 2004, accepted 15 October 2004.

In cooperatively breeding birds, more than two adults participate in a single breeding event, either by defending the nest, incubating eggs, or provisioning young (Brown 1987). This is the predominant social system in 18.5% of oscine passerine species with biparental care (383 of 2,067 species), and occurs occasionally in another 3.7% of oscines classified as pair breeders (Cockburn 2003). However, patterns of nestling care are unknown for most passerines ($n = 2,385$), particularly those in the Neotropics (Cockburn 2003); thus, cooperative breeding may occur in still other species. Intensive studies of populations of banded birds are needed to determine the extent of pair versus cooperative breeding in these species.

Cooperative breeding may arise in several different ways, including when (1) independent offspring remain on natal territories until their parents' next breeding period (Cockburn 1998), (2) individuals initially disperse and then preferentially immigrate into social groups composed of related individuals (Baglione et al. 2003), and (3) groups of unrelated individuals reproduce together (Davies 1992). In the first case, delayed dispersal by offspring is a necessary prerequisite for cooperation. However, in some species in which offspring remain on their natal territories for extended periods, helping never occurs (reviewed in Ekman et al. 2001). Delayed dispersal by off-

spring is often associated with high adult survival, low reproductive rates, and deferred maturation (Brown 1987), and may be a form of extended parental investment, in which parents permit or encourage offspring (via access to resources) to remain on natal territories (Ekman et al. 2001).

Wrens (Family Troglodytidae) have been among the most studied New World avian taxa in terms of cooperative breeding, with much of this research focusing on the genus *Campylorhynchus*, in which 9 of 13 species are known to breed cooperatively (e.g., Austad and Rabenold 1986, Rabenold 1990). Cooperative breeding occurs regularly in Black-capped Donacobius (*Donacobius atricapillus*) and has been reported in House Wrens (*Troglodytes aedon*; reviewed in Cockburn 2003). However, the breeding systems of most species in this family, especially those in tropical areas, have not been described and cooperative breeding may be more common than reported. For example, many species in other genera, in particular *Thryothorus*, are often found in family groups (e.g., Skutch 1960, 2001; Slud 1964; Hilty and Brown 1986; Brewer 2001), suggesting that independent offspring may stay on natal territories for extended periods, potentially setting the stage for cooperative breeding. Here, I describe the first record of cooperative breeding in the genus *Thryothorus* made during a study of patterns of nestling provisioning in Buff-breasted Wrens (*T. leucotis*; SAG unpubl. data). Previous studies have reported that Buff-breasted Wrens are often found in groups of 3–4 individuals (Skutch 1968, Farabaugh 1983, Ahumada 2001), but none has recorded dis-

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persal delayed into the breeding season or cooperative breeding.

METHODS

Buff-breasted Wrens are small (16–23 g), monochromatic birds that inhabit secondary forest throughout their range from central Panama to northern South America (Ridgely and Tudor 1989). They maintain territories and partnerships throughout the year, and breed during the wet season (April to October; SAG unpubl. data); initiation of breeding is closely tied to the onset of rains (Ahumada 2001). Buff-breasted Wrens are socially and genetically monogamous: extra-pair young were detected in only 1 of 31 broods (Gill et al. 2005). Throughout the year, pairs produce antiphonal duets in which males and females give alternating sex-specific songs (Farabaugh 1983).

I studied a color-banded population of Buff-breasted Wrens in Gamboa, Republic of Panama (9° 7' N, 79° 42' W) during both dry and wet seasons (February–May 1997, February–July 1998, October 1998, February–June 1999). The study site was a 22-ha secondary forest bordered on three sides by Gamboa, the Rio Chagres, and the Panama Canal, and it was separated from the nearest forest by a 100-m grassy marsh. In 1997, both individuals in 15 of 18 pairs were banded, whereas in 1998 ($n = 24$) and 1999 ($n = 19$), both members of all pairs were banded. I banded a total of 65 adults, 17 adult philopatric offspring, 27 fledglings, and 13 nestlings. I sexed individuals based on body size (females are smaller than males; SAG unpubl. data), singing behavior (Farabaugh 1983), and egg laying and incubation (Gill 2003). When more than two adult birds resided on a given territory, I distinguished paired adult birds from their adult philopatric offspring by behavior, as paired individuals duetted more frequently, and spent more time in close association (<5 m apart) than with their offspring. I defined a philopatric offspring as one that remained on its natal territory for >3 months.

Buff-breasted Wrens typically construct separate dormitory nests—in which they roost overnight—and breeding nests, although approximately 10% of dormitory nests are used for breeding (SAG unpubl. data). I located nests by searching areas from which pairs

gave their first song of the morning (these are typically given when birds are close to their nests), during regular searches of territories, and by following individuals that were collecting or holding nesting materials. I did not mark nest locations, as they were easy to re-find. Nests were checked every 2 days until clutch completion (modal clutch size = 3, range = 2–3, $n = 42$) and irregularly thereafter until the young fledged or the nest failed.

As part of a broader study examining male and female effort during nest construction and nestling provisioning, I made 1-hr observations of nestling provisioning every 2 days from the day after hatching (day 0) until the nestlings fledged (usually day 15). All observations were performed between 06:00 and 14:00 EST, from a position at least 5 m from nests, to avoid influencing the behavior of the parents as they returned to feed or brood (females only). During these observations, I quantified the number of visits per hour by male and female parents, as well as visits by the retained offspring. In addition, I noted the singing behavior of offspring, as well as aggressive interactions between them and their parents.

RESULTS

Of 57 offspring banded as nestlings, fledglings, or independent birds, 35 remained on their natal territories for >3 months after fledging. Another six unbanded individuals lived on territories with banded adults. I assumed that these unbanded individuals were the offspring of the banded adults because (1) their presence was consistent with the fledging of offspring in those territories in the previous breeding season; (2) 17 individuals, banded as adults and residing on territories with 2 other adult birds, were the genetic offspring of those adults (SAG unpubl. data); and (3) I have no evidence that groups formed other than by the retention of offspring. Thus, a total of 41 offspring (65.1% of offspring fledged) remained on their natal territories for >3 months. Prior to their parents' next breeding attempt, most philopatric offspring either dispersed to become territory holders in the study population ($n = 13$) or disappeared ($n = 24$). Only four individuals (9.8% of philopatric offspring) postponed dispersal for >1 year, staying on

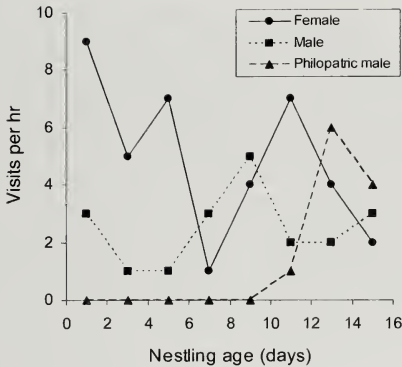


FIG. 1. Pattern of provisioning by a single pair of Buff-breasted Wrens and a philopatric, unbanded male when feeding three nestlings. Eggs hatched on day 0 and were observed every second day from days 1 to 15, at which time the young fledged. The philopatric male was not observed within 5 m of the nest area prior to day 11.

their natal territories through their parents' subsequent breeding season.

Between 6 and 10 June 1999, I observed helping at the nest by an unbanded male during the second breeding attempt of a banded pair that had been together for >2 years. This pair had fledged two males in the previous breeding season, one of which I captured and banded. Both male offspring were present on the territory at the start of my field season in February 1999, with the banded male dispersing to another territory before breeding commenced. The unbanded male was last observed on his natal territory on 30 June, a date that corresponded to the end of my field season.

Visitations by the parents and the unbanded male while provisioning a brood of three nestlings are summarized in Figure 1. Between days 1 and 9 after hatch, the unbanded male was not observed within 10 m of the nest, but often sang within the territory. On day 11 near the start of observations, the unbanded male entered the nest and stayed in it for approximately 10 sec. Shortly after the unbanded male left the nest there was a chase involving two unidentified wrens, and "aggressive" churring (such calls are heard only during aggressive encounters; SAG pers. obs.). Less than 30 sec later, a third unidentified wren approached this pair, and another chase ensued. The parental male did not visit the nest within

30 min of this interaction, while the female visited the nest four times within that period. Near the end of the 1-hr observation period, the unbanded male, with food in his bill, tried to approach the nest once more. The parental male was in the nest, exited it and then chased the unbanded male away from the nest. Soon after, the parental male and the unbanded male were observed foraging within 2 m of each other.

On day 13, the unbanded male visited the nest six times within an hour, equaling the contribution of the parents combined. His first visit was apparently undetected by the parents as they were not in the immediate nest area at the time. While approaching the nest for his second visit, the unbanded male was supplanted by the male parent, who gave an aggressive churr, but the unbanded male was not chased out of the area. Rather, he continued to move around the nest, with the male parent following 1–2 m behind. The unbanded male then entered the nest and fed the young. On the next four visits, the unbanded male was followed several times by the male parent, but no aggression was exhibited. On the day of fledgling (day 15), the unbanded male made four visits to the nest, more than the individual effort of either parent (Fig. 1). No aggression between the unbanded male and the parental male was observed at this time, and no aggression between the unbanded male and the female was ever recorded. Three young fledged from the nest on 10 June. I made three additional untimed observations of this pair after the young fledged, during which the unbanded male perched within 2 m of the fledglings and their parents, and once fed the fledglings.

During observations at a second nest in June 1999, I witnessed aggressive encounters between a banded female offspring (hatch year 1998) and her banded father around the breeding nest, but never observed the female enter the nest to feed the young. On day 5, the philopatric female approached within 5 m of the nest and was chased by the male 3–4 times. She moved to 2 m from the nest and was chased again by the male parent, who gave several aggressive churrs. When the nestlings were 13 days old, the philopatric female perched 4–5 m from the nest and was immediately chased by the male, who uttered

aggressive churrs (the philopatric female did not approach the nest during observations made before day 5, between days 7 and 11, or on day 15). Two nestlings fledged on 6 June, and I observed the philopatric female within 3 m of them on the day of fledging as well as during observations 2 weeks later. At both times, the family was in thick vegetation and I made few definitive observations of feeding by any adult. No aggression was noted between the male and the philopatric female after the young fledged, nor was aggression observed at any time between the parental and philopatric females.

Two other banded offspring were observed on their natal territories during subsequent breeding attempts of their banded parents, but helping was not observed. I observed a banded, second-year female offspring on her natal territory 1 day before her parents began constructing their second breeding nest, but did not see her during 4 hr of observation of nestling provisioning. However, this female apparently stayed on her natal territory while her parents bred, as she was observed with them in the post-breeding season. Finally, a banded male was observed repeatedly foraging and singing with his banded parents over the course of their four breeding attempts. The philopatric male built a dormitory nest with his father (while the female incubated eggs), but did not participate in the construction of two breeding nests during timed observations. Although I did not observe this pair during nestling provisioning, the male offspring was still present on the territory at that time.

DISCUSSION

The potential for observing cooperative breeding in Buff-breasted Wrens was low, as only 4 of 41 independent offspring postponed dispersal for >1 year. All four offspring that delayed dispersal may have participated in territorial defense by singing on their own or with their parents. One male helped by feeding young, and one female appeared to try to provision nestlings and may have successfully fed fledglings. The latter cases were marked by aggression by male, but not female, parents toward their adult offspring during the nestling period. Similar aggressive interactions between parents and non-breeders occur in some small-bodied corvids during nestling

care to prevent non-breeders from accessing nests, possibly to decrease activity around the nest and thereby minimize the risk of nest predation (Strickland and Waite 2001). Considering pair-breeding species in the Neotropics, Skutch (1949) proposed that nest predation increases with the rate at which parents feed the nestlings (see Martin et al. 2000). Thus, male parents may have behaved aggressively toward their offspring to stop them from visiting nests. Interestingly, in the one case of cooperative breeding I observed, parents appeared to visit their nest less once their male offspring started to provision the young (Fig. 1). Alternatively, parental aggression toward philopatric offspring may occur when resources become depleted and competition for the remaining resources intensifies (Strickland and Waite 2001). This hypothesis seems unlikely to apply to Buff-breasted Wrens, as breeding occurs during the wet season, when arthropod prey are abundant (e.g., Wolda 1996). Prey depletion seems more likely to occur during the dry season, yet I witnessed little or no parental aggression toward philopatric offspring at that time.

Most offspring that delayed dispersal did not stay on their natal territories long enough to help with reproductive activities of their parents. On average, offspring dispersed just prior to the onset of their parents' reproductive period (SAG unpubl. data). Prior to dispersing, however, some offspring participated in the construction of dormitory nests, and most sang either as part of territory defense or to advertise themselves to potential mates. Further studies are needed to determine the role of offspring in these activities, as well as the benefits and costs of philopatry for both parents and their offspring. The phenomenon of delayed dispersal in the absence of cooperative breeding is underappreciated, yet its study is a logical step toward understanding the evolution of cooperation (Brown 1987). The monophyletic wren family (Barker 2004) offers an exceptional opportunity to study the evolution of delayed dispersal and cooperative breeding due to the diversity of breeding and dispersal patterns, ranging from pair breeders with early dispersal by juveniles, to those with delayed juvenile dispersal without cooperation, to truly cooperative breeders.

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BREEDING BIOLOGY OF THE ENDANGERED ROTA BRIDLED WHITE-EYE

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ABSTRACT.—Little is known about the breeding biology of Bridled White-eyes (*Zosterops conspicillatus*), especially the federally endangered Rota Bridled White-eye (*Z. c. rotensis*). Here, we report on the breeding behavior, nest-site characteristics, and nest dimensions of Rota Bridled White-eyes. From 1997 to 1999, we found 20 Rota Bridled White-eye nests in *Elaeocarpus joga* (35%), *Hernandia labyrinthica* (30%), *Merrilliodendron megacarpum* (20%), and introduced *Acacia confusa* (15%) trees between 320 and 460 m in elevation. Nests were 2.5–12.8 m above the ground ($n = 18$) in trees 3.3–14.6 m tall ($n = 16$). Clutch size ranged from one to two eggs ($n = 7$) and the breeding season was from at least December through August. Nest dimensions ($n = 4$) were 36–44 × 57.7–60.8 mm (outer height × diameter) and 25–29 × 44.6–47.7 mm (cup depth × diameter). Received 1 April 2004, accepted 4 October 2004.

The Bridled White-eye (*Zosterops conspicillatus*) is a small bird (~10 g) endemic to the Mariana Islands in the tropical western Pacific Ocean. Currently, the species is divided into three subspecies found on the islands of Guam (*Z. c. conspicillatus*); Saipan, Tinian, and Aguiguan (*Z. c. saypani*); and Rota (*Z. c. rotensis*; hereafter referred to as Guam, Saipan, and Rota Bridled White-eyes, respectively; Stresemann 1931). Recent genetic work (Slikas et al. 2000) and observed differences in plumage, vocalizations, and behavior (Pratt et al. 1987, Collar et al. 1994), suggest that the Rota Bridled White-eye may warrant species status.

The Saipan Bridled White-eye is abundant and widespread on the islands of Saipan (2,221 birds per km²), Tinian (2,931 birds per km²), and Aguiguan (1,930 birds per km²; Engbring et al. 1986). Historically, the Guam Bridled White-eye also was believed to be abundant and widespread (Jenkins 1983), although no island-wide surveys were ever completed. After the introduction of the

brown treesnake (*Boiga irregularis*), however, the Guam Bridled White-eye population rapidly declined and the subspecies is presumed extinct (Wiles et al. 2003).

The first published record that detailed locations of the Rota Bridled White-eye was of four birds collected by Navy personnel at two low-elevation (0–150 m) areas (Songsong Village and Malilok Point) in 1945 (Baker 1948). Baker (1948) considered the Rota Bridled White-eye “numerous,” though no surveys were conducted and bird collection was primarily limited to low-elevation areas. By 1975, the Rota Bridled White-eye population was limited to high-elevation areas in the Sabana region, a plateau 450 m in elevation dominating the topography of the western half of Rota (Pratt et al. 1979). In 1982, the first island-wide, avifaunal survey was completed and the Rota Bridled White-eye population was estimated to be approximately 10,000 birds (183 birds per km²); it was primarily restricted to high-elevation areas of the Sabana region (Engbring et al. 1986). By 1996, the population was estimated to be approximately 1,000 birds and was further restricted to cliff-line forest in the Sabana region (Fancy and Snetsinger 2001). The cause of this decline is uncertain; however, predation by the introduced Black Drongo (*Dicrurus macrocercus*) and habitat changes appear to be important factors (Craig and Taisacan 1994, Craig 1999, Amidon 2000, Fancy and Snetsinger 2001). Currently, the Rota Bridled White-eye is listed as endangered under the Endangered Species Act (U.S. Fish and Wildlife Service 2004) and

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critically endangered by the World Conservation Union (2003).

The paucity of life history information about the Rota Bridled White-eye makes it difficult to determine the specific cause of decline. Data on breeding biology are especially limited, as only brief descriptions of three nests have been reported (Yamashina 1932, Pratt 1985, Lusk and Taisacan 1997). Data on incubation, nestling, and fledgling periods, as well as on parental care do not exist. Further, information on the breeding biology of Bridled White-eyes on Saipan and Guam also is very limited. In this paper we report, often for the first time, information on nest-site characteristics, nest dimensions, and breeding behavior of Rota Bridled White-eyes.

METHODS

Observations of all nests were made on the island of Rota (14° 10' N, 145° 12' E), Commonwealth of the Northern Mariana Islands (CNMI). Rota is approximately 86 km² and has a maximum elevation of 490 m. The island is composed of a series of upraised, coral limestone plateaus formed on an extinct volcanic peak. We conducted our field work primarily within the current range of the Rota Bridled White-eye, from 300 to 450 m in elevation in the Uyulan Hulo, Applatagua, Finata, and Alesna regions from June to August 1998 and from January to August 1999. The climate in the CNMI is tropical, with mean temperatures of 24 to 32° C, high humidity, and average rainfall of 200 to 260 cm (National Oceanic and Atmospheric Administration 1998).

We found nests by actively searching areas used by Rota Bridled White-eyes and by monitoring the movements of individuals carrying nesting material or food items. We monitored all active nests at least every 4 days, using either a mirror on a telescoping pole or a spotting scope. When possible, we recorded clutch size, number of hatchlings and fledged young, and assessed reasons for nest or clutch failure. Because Rota Bridled White-eyes are sexually monomorphic in plumage and none of the adults at active nests was color-banded, sexes could not be identified; however, we recorded observations of switching and simultaneous feeding by both adults to determine the involvement of both sexes in incubation, brood-

ing, and feeding of nestlings and fledglings. When nests were accessible, we attempted to band nestlings with U.S. Geological Survey aluminum bands and distinct combinations of color bands.

At all nests we measured diameter at breast height (dbh) of the nest tree, height of the nest in the tree, nest tree height, tree species (based on the taxonomic classification of Raulerson and Rhinehart 1991), distance from nest to bole, and elevation. When nests were accessible, we also recorded nest dimensions and nest material used. For nest dimensions, we recorded cup diameter and depth, and outside nest diameter and height. Means are presented \pm SE.

RESULTS

We found 19 Rota Bridled White-eye nests during the 1998 (June to August) and 1999 (January to August) field seasons. An additional nest was found in December 1997 during preliminary field work (S. M. Plentovich pers. comm.). Ten of the nests were active, and of these, seven produced one or two fledglings. Of the three active nests that failed, one appeared to be depredated at the nestling stage, the 1997 nest was destroyed during Typhoon Paka in December 1997, and the third was depredated or abandoned, possibly due to observer disturbance. Ten nests were considered inactive but were distinguishable from other passerine nests, including those of the Micronesian Honeyeater (*Myzomela rubrastra*), based on nest structure, composition, and placement within the nest tree and our observations of Rota Bridled White-eye activity at the nest site.

We found active nests in December ($n = 1$), March ($n = 4$), May ($n = 2$), July ($n = 2$), and August ($n = 1$). Fledging dates of two nests indicate that breeding also occurs in April and June. In addition, we observed what appeared to be two recently fledged Rota Bridled White-eyes (no eye-rings and a scruffy appearance) in late January.

Rota Bridled White-eye eggs were light blue and unmarked; clutch size for seven nests ranged from one to two eggs, and we documented the fledging of two nestlings from one nest. Based on our observations at seven active nests, incubation and nestling periods appeared to be at least 10 and as long as 12 days.

During the incubation and nestling stages, we observed both adults incubating eggs and brooding nestlings, and both simultaneously provisioning nestlings. We banded one nestling and documented a post-fledging parental care period of at least 8 days. The banded nestling was seen approximately 10 m from the nest with both adults and another young bird, possibly its nest mate, which had fledged prior to banding. Both birds were observed actively begging (calling and quivering their wings) from both adults and did not appear to be foraging, although they flew and hopped among the branches of trees. We also observed adult Rota Bridled White-eyes constructing and cleaning (eating fecal sacs) nests, but did not observe both adults simultaneously building nests or taking part in nest sanitation.

We found Rota Bridled White-eye nests at 320–460 m in elevation in the native tree species *Elaeocarpus joga* ($n = 7$), *Hernandia labyrinthica* ($n = 6$), and *Merrilliodendron megacarpum* ($n = 4$), and in the introduced *Acacia confusa* ($n = 3$). Mean height of nests above ground ($n = 18$) was $8.3 \text{ m} \pm 0.7$ (range: 2.5–12.8 m). Mean height of nest trees ($n = 16$) was $10.3 \text{ m} \pm 0.8$ (range: 3.3–14.6 m), and mean dbh of nest trees ($n = 17$) was $29.9 \text{ cm} \pm 40.2$ (range: 2.3–60.2 cm). Mean distance from tree bole to nest ($n = 17$) was $3.1 \text{ m} \pm 0.4$ (range: 0.9–6.7 m).

All Rota Bridled White-eye nests were cup-like and the nests found in *E. joga*, *M. megacarpum*, and *A. confusa* trees were all suspended between branches and branchlets. Five of the six nests found in *H. labyrinthica* were suspended between branches and leaf petioles. The remaining nest was suspended from *Davallia solida* ferns below a *H. labyrinthica* branch.

We measured nest dimensions of four Rota Bridled White-eye nests. Mean outer height was $40.0 \text{ mm} \pm 1.0$ (range: 36.0–44.0 mm) and cup depth was $28.0 \text{ mm} \pm 1.0$ (range: 25.0–29.0 mm). Mean cup diameter was $45.9 \text{ mm} \pm 0.7$ (range: 44.6–47.7 mm) and outer nest diameter was $59.0 \text{ mm} \pm 0.7$ (range: 57.7–60.8 mm). All nests appeared to be composed of rootlets, woven grass or *Pandanus* spp. fibers, spider webs, light green moss, and a yellow, cottony material. The inner cup appeared to be composed of woven grass or

Pandanus spp. fibers. We also observed a Rota Bridled White-eye recycling old nest material to build a new nest; we did not observe white-eyes reusing nests.

DISCUSSION

Previously described nest-site characteristics and nest dimensions (Yamashina 1932, Pratt 1985, Lusk and Taisacan 1997) are similar to what we found. Of the three nests previously reported, only two indicated the tree species in which the nests were found. One nest was in *H. labyrinthica* (Lusk and Taisacan 1997) and the other was in *Hernandia* spp. (presumably *H. labyrinthica*; Pratt 1985). Both nests were also found in areas dominated by *H. labyrinthica*/E. *joga* mixed forest at $>240 \text{ m}$ in elevation. In our study we observed the use of three additional tree species, including one introduced species, *A. confusa*; we found 35% of our nests in two additional forest types (*M. megacarpum* and *A. confusa* forests). Lusk and Taisacan (1997) report that the Rota Bridled White-eye breeding season extends from at least March until June. Our observations indicate a breeding season from at least December through August. However, the species probably breeds year-round, as was reported for the Guam Bridled White-eye (Marshall 1949, Jenkins 1983), because nesting was observed in both the wet and dry seasons.

There is little published information on the nests of Saipan and Guam Bridled White-eyes. Yamashina (1932) reported clutch size (1–3 eggs), nest dimensions (40–55 mm outer nest height, 25–30 mm cup depth, 55–65 mm outer diameter, and 40–45 mm cup diameter), nest heights (2–4 m), and nest tree species (*Pithecellobium* spp.) for three Saipan Bridled White-eye nests found on Tinian. Seale (1901) reported nest dimensions (48 mm outer height, 41 mm outer diameter, and 25 mm cup depth) and nest tree species (*Pithecellobium dulce*) for one Guam Bridled White-eye nest. Jenkins (1983) reported on clutch size (2 eggs), nest dimensions (40–50 mm nest diameter and 70–80 mm “deep”), nest height (2.4 m), and nest tree species (*Leucaena leucocephala*) for one Guam Bridled White-eye nest. Hartert (1898) reported on clutch size (2–3 eggs), nest width (50–80 mm), and nest height (1–2 m) for “several” Guam Bridled White-eye nests.

Three active Saipan Bridled White-eye nests were reported at 2.3–6 m above ground in *Casuarina equisetifolia* and *Phragmites karka* (N. C. Johnson unpubl. data).

Overall, the clutch size and nest dimensions we found for the Rota Bridled White-eye are within the range of those reported for both the Saipan and Guam Bridled White-eye. Height above ground of Guam and Saipan Bridled White-eye nests is generally lower (≤ 6 m) than what we found for the Rota Bridled White-eye. Differences may be due to the limited sample of Guam and Saipan Bridled White-eye nests. Interestingly, all of the identifiable plant species used as nest substrate by Guam and Saipan Bridled White-eyes were introduced to the Mariana Islands, whereas no Rota Bridled White-eye nests were found in any of these plant species. This apparent difference in use of nest substrate is also likely due to the limited sample of Guam and Saipan Bridled White-eye nests.

No information on incubation or nestling and post-fledging parental care periods is available for Bridled White-eyes on Saipan, Tinian, or Guam. Incubation and nestling period data are known for Pale White-eye (*Zosterops pallidus*), Silvereye (*Z. lateralis*), and Japanese White-eye (*Z. japonicus*). The Pale (Broekhuysen and Winterbottom 1968) and Japanese White-eyes (Isobe 1997) have 10–12 day incubation and 10–12 day nestling periods, but the Silvereye has incubation and nestling periods of 12–14 days each (Kikkawa and Wilson 1983). The estimated duration of post-fledging parental care is approximately 2 weeks for the Silvereye (Kikkawa and Wilson 1983) and 15–20 days for the Japanese White-eye (van Riper 2000). Based on this information, the Rota Bridled White-eye's period of post-fledging parental care may be substantially longer than the 8 days we observed; more observations are needed.

Kikkawa and Wilson (1983), report that the eye-ring on recently fledged Silvereye chicks develops after a 1-week period. Van Riper (2000) reports an eye-ring development period of 23 days for the Japanese White-eye. Our observations of one banded fledgling indicated that the eye-ring had not completely developed 8 days after fledging.

Our observations of nest and fledgling attendance reveal that both sexes participate in

incubation, brooding, and feeding of nestlings and fledglings. This parallels the behavior of many other white-eye species (Broekhuysen and Winterbottom 1968, Ali and Ripley 1974, Kikkawa and Wilson 1983, van Riper 2000). In most species of white-eyes studied to date, both sexes also participate in nest construction (but see Ali and Ripley 1974). Overall, the breeding behavior of the Rota Bridled White-eye appears similar to that of other white-eye species.

We found Rota Bridled White-eye nests in *H. labyrinthical*/E. *joga* mixed forest, *M. megacarpum* forest, and introduced *A. confusa* forest only at high elevations (>200 m). Each forest type comprised primarily tall trees (10 m) that were large in diameter (>10 cm; Amidon 2000), and all forests were considered wet forests (Fosberg 1960, Falanruw et al. 1989). Although apparently suitable low-elevation white-eye habitat exists on Rota, white-eyes are now restricted to mature forests at higher elevations for reasons that are unclear.

We recommend additional research on the breeding ecology of Rota Bridled White-eyes and comparisons of their breeding ecology with that of the Saipan Bridled White-eye. The information we obtained in our study was limited; additional research may provide more insight into why the Rota Bridled White-eye is declining—and restricted to high-elevation habitats—and provide valuable information to help manage and recover this critically endangered species.

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PREY OF BREEDING CHILEAN HAWKS (*ACCIPITER CHILENSIS*) IN AN ANDEAN *NOTHOFAGUS* FOREST IN NORTHERN PATAGONIA

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ABSTRACT.—We quantified the diet of the Chilean Hawk (*Accipiter chilensis*) by analyzing 495 prey remains collected during two breeding seasons (2001–2002 and 2002–2003) in an Andean *Nothofagus* forest of Nevados de Chillán, northern Patagonia. The diet was almost exclusively birds (97.8% of all prey remains), with relatively few rodents (1.6%) and insects (0.6%). At least 19 vertebrate species composed the prey remains (1 small mammal and 18 bird species), with Austral Thrush (*Turdus falcklandii*), White-crested Elaenia (*Elaenia albiceps*), Black-chinned Siskin (*Carduelis barbata*), Fire-eyed Diucon (*Xolmis pyrope*), and Thorn-tailed Rayadito (*Aphrastura spinicauda*) being the most common. All identified vertebrate prey are known to use forest habitats; 47% ($n = 9$) are forest specialists. Prey that inhabit both forest and shrublands accounted for 82% of the remains, and 18% of prey remains were of forest specialists. Our results indicate that during the breeding season, Chilean Hawks in Nevados de Chillán are pre-eminent, bird-eating predators that feed primarily on forest-dwelling birds. Received 25 February 2004, accepted 12 October 2004.

The loss of old-growth, native forests is the most serious threat to the flora and fauna of the Patagonian temperate forest region (Fuentes 1994). The endemic, forest-specialist fauna—including various raptors (Jaksic and Jiménez 1986, Stotz et al. 1996)—is the most critically threatened (Willson et al. 1994, Kelt 2001). However, the secretive behavior and low population densities of forest raptors, and the complexity of their habitats, make them very difficult to study (Thiollay 1996, Bierregaard 1998). With the exception of the Rufous-legged Owl (*Strix rufipes*; Martínez and Jaksic 1996, 1997; Díaz 1999), Chilean forest raptors are not well-studied. Because raptors are top-level predators and generally have large home ranges, an understanding of their ecological requirements is crucial, particularly for those that are habitat specialists (Bierregaard 1998).

The Chilean Hawk (*Accipiter chilensis*; Thiollay 1994) is one of the least studied raptors in the Patagonian temperate forest. This hawk has been listed as rare throughout its entire range (Jaksic and Jiménez 1986), although it is considered relatively common in

the Cape Horn province (Venegas and Sielfeld 1998). Its populations are considered threatened due to increasing habitat loss from extensive fires, logging pressures, and hunting (Jaksic and Jiménez 1986). Most of what we know of the Chilean Hawk's biology is descriptive (e.g., Housse 1945, Johnson 1965); what is known about its habitat, feeding, breeding, and movements was summarized by Thiollay (1994). Here, we report on the Chilean Hawk's diet during the breeding season in the Andean *Nothofagus* forest of Nevados de Chillán, northern Patagonia.

METHODS

Our study was conducted in the Huemules del Niblinto Nature Sanctuary and National Reserve (36° 45' S, 71° 29' W; 50 km east of Chillán), located in northernmost Patagonia (36–56° S; see Vuilleumier 1985). Niblinto is a private/public wildlife area (~10,000 ha) that forms part of the Nevados de Chillán, a priority site for biodiversity conservation in Chile (Muñoz et al. 1996). The landscape around the Nevados de Chillán is rugged, composed of fairly narrow valleys and high hills (800–2,500 m elevation, $\geq 45^\circ$ slopes). The climate is Mediterranean, characterized by dry, warm (20–30° C) summers and cold (0–10° C), wet (rainy and snowy) winters (mean annual precipitation >1,000 mm).

In February 2000, we began an ecological study of high-Andean and forest raptors of

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Nevados de Chillán. Our objectives were to (1) determine their diets and relationships to prey abundance, (2) describe their breeding biology, and (3) study their hunting behavior. We studied the diet of breeding Chilean Hawks from prey remains collected during the austral summers of 2001–2002 and 2002–2003 at two nest sites (A and B; 7 km apart) located along the Niblinto river valley. This valley is dominated by shrublands and second-growth, mixed-deciduous forest composed of *Nothofagus dombeyi*, *N. obliqua*, *N. alpina*, and *Podocarpus saligna*. The older trees can reach 20–30 m in height and 0.5–1.1 m in diameter; canopy cover ranges from 50 to 85%. The midstory is composed principally of native bamboo (*Chusquea* spp.; 2–3 m tall) and dispersed shrubs (e.g., *Luma apiculata*, *Ribes magellanica*, *Azara lanceolata*, *Fuchsia magellanica*; 1–2.5 m tall). The understory is composed of diverse herbs, shrubs, and tree saplings. In addition, there are many old, fallen trees (0.5–1.5 m in diameter). During the 1950s and 1960s, some forested areas were cleared by both logging and fire to create pasturelands. These previously cleared areas are now covered by dense shrublands composed of *Nothofagus* tree saplings and pioneering species of high-Andean shrubs (*Berberis* spp., *Pernettya* spp., *Baccharis* spp.). The proportions of forest and shrubland in Niblinto are about 60 and 40%, respectively.

Prey remains at nest site A were collected during 18–25 February 2002 (fledgling period), 8–10 December 2002 (incubation period), 22 January–5 February 2003 (brood-rearing period), and 7–26 February 2003 (fledgling period). At nest site B, remains were collected only during 18–25 February 2002. Each day we searched for prey remains under nests (16–18 m above ground) and under all trees considered to be potential plucking posts (10–20 m tall). We collected feathers, feet, carcasses, skulls, bills, and fur. Most samples were collected at specific locations (within a 1- to 2-m radius) and generally, remains were from one prey item. When samples contained feathers of >1 avian species, they were analyzed in the laboratory. If >1 species was identified in a sample, each was considered a separate prey remain. On each sampling day, we collected all remains found to avoid duplication in subsequent collections. Because plucked

feathers that caught on branches may have been dislodged later by wind, it is probable that a fraction of our samples were duplicated. It was not possible to discriminate prey remains with respect to the sex or age of the hawk that captured them.

Remains of birds and small mammals were identified using reference material at the Zoology Institute and the Ecology and Evolution Institute, University Austral, Chile. We identified prey items to the lowest possible taxonomic category; bird species were identified by feather color, small mammals by hair color or molar structure, and insects by head capsules or elytra (according to keys in Peña 1986). Because Chilean Hawks plucked and quartered vertebrate prey at a number of plucking posts (especially large prey), our samples were not independent; therefore, a single set of prey remains could not be assumed to represent the entire individual prey item. Studies of prey remains may overestimate the numbers of birds and underestimate the numbers of smaller prey, such as lizards or insects (e.g., Watson et al. 1998); thus, we quantified dietary components as a percentage of occurrence for a given taxon (Fo) by dividing the number of remains of that taxon by the total number of prey remains for all taxa (Marti 1987). We further evaluated the diet of Chilean Hawks with respect to the preferred habitats of their prey. Prey species exclusively or primarily inhabiting forest were classified as forest specialists, and those occupying both forests and shrublands were classified as forest/shrubland dwellers.

RESULTS

We collected 495 samples of prey remains (488 at site A and 7 at site B). We identified 18 bird and 1 mammal species (Table 1). Passerines were the dominant bird prey, with Austral Thrush (*Turdus falcklandii*), White-crested Elaenia (*Elaenia albiceps*), Black-chinned Siskin (*Carduelis barbata*), Fire-eyed Diucon (*Xolmis pyrope*), and Thorn-tailed Rayadito (*Aphrastura spinicauda*) being the most common (Table 1). The occurrence of rodents (1.6%) and insects (0.6%) in the diet was negligible. Of the 19 vertebrate prey identified to species, 47% ($n = 9$) were forest specialists and 53% ($n = 10$) inhabit both forests and shrublands (Table 1). By occurrence, the

TABLE 1. Diet of breeding Chilean Hawks (*Accipiter chilensis*) based on prey remains collected during the breeding seasons of 2001–2002 and 2002–2003 from two nest sites in an Andean *Nothofagus* forest, Nevados de Chillán, northern Patagonia. Fo = percentage of occurrence, *n* = number of prey remains.

Prey species	Mass (g) ^a	Habitat ^b	Fo (<i>n</i>)
Mammals			
<i>Abrothrix longipilis</i>	30	F	1.0 (5)
Unknown Sigmodontinae			0.6 (3)
Birds			
<i>Enicognathus ferrugineus</i>	170	F	0.2 (1)
<i>Picooides lignarius</i>	42	F	1.0 (5)
<i>Colaptes pitius</i>	330	F, S	0.4 (2)
<i>Cinclodes patagonicus</i>	50	F, S (A)	0.2 (1)
<i>Aphrastura spinicauda</i>	11	F	3.0 (15)
<i>Leptasthenura aegithaloides</i>	9	F, S	0.2 (1)
<i>Pygarrhichas albogularis</i>	23	F	1.8 (9)
Unknown Furnariidae			0.4 (2)
<i>Pteroptochos castaneus</i>	110	F	1.8 (9)
<i>Scelorchilus rubecula</i>	60	F	2.0 (10)
<i>Scytalopus magellanicus</i>	12	F	0.2 (1)
Unknown Rhinocryptidae			1.4 (7)
<i>Xolmis pyrope</i>	36	F, S	6.7 (33)
<i>Elaenia albiceps</i>	16	F, S	17.0 (84)
<i>Colorhamphus parvirostris</i>	11	F	0.2 (1)
Unknown Tyrannidae			0.8 (4)
<i>Troglodytes aedon</i>	10	F, S	0.4 (2)
<i>Turdus falcklandii</i>	87	F, S	18.4 (91)
<i>Curaeus curaeus</i>	90	F, S	0.4 (2)
<i>Phrygilus patagonicus</i>	38	F, S	1.8 (9)
<i>Carduelis barbata</i>	15	F, S	7.1 (35)
Unknown Fringillidae			1.8 (9)
Unknown Passeriformes			27.0 (133)
Other, unknown birds			3.6 (18)
Insects			
<i>Aeshna</i> spp.			0.2 (1)
Coleoptera			0.4 (2)
Total prey remains			495

^a Weights for *E. ferrugineus*, *C. pitius*, *C. patagonicus*, *P. albogularis*, and *S. magellanicus* were given by R. P. Schlatter (pers. comm.); weights for remaining species were taken from Jiménez and Jaksic (1989) and Egli (1996) for birds, and from unpublished data of the authors for small mammals.

^b Habitat types from Rozzi et al. (1996) for birds and from the authors' unpublished data for small mammals: A = aquatic, F = forest, S = shrubland.

forest/shrubland dwellers were the most common prey (Fo = 82%); the remaining 18% were forest specialists.

DISCUSSION

The Chilean Hawk has been described as a bird-eating predator (Housse 1945, Johnson 1965). Our finding that birds—the Austral Thrush in particular—constitute the main prey of the Chilean Hawk concurs with a previous report by Housse (1945). Although the Chilean Pigeon (*Columba araucana*) has been described as one of the Chilean Hawk's main prey species (Johnson 1965), no pigeon re-

mains were found in our collections, due, perhaps, to the low abundance of Chilean Pigeons at our study site (<1% of all counted birds; RAFR unpubl. data) and/or to the fact that we collected most prey remains from only one nest site. Our finding of various rodents among prey remains contradicts a previous assertion that the Chilean Hawk is strictly a bird-eating raptor (Housse 1945, Johnson 1965) and supports Figueroa et al. (2001), who reported yellow-nosed field mouse (*Abrothrix xanthorhina*) in the diet of Chilean Hawks in *Nothofagus* forests of Tierra del Fuego. Although lizards are relatively

common in our study area, we did not find lizard remains among our samples—most likely because lizards are consumed whole by Chilean Hawks (as we occasionally observed after this study). During February 2004 near nest site A, SCS observed a juvenile Chilean Hawk capture and swallow a lizard whole (*Liolaemus* spp., 13–14 cm length).

The most common prey items in the Chilean Hawks' diet appeared to represent the most abundant species at our study site. Thorn-tailed Rayadito, White-crested Elaenia, Black-chinned Siskin, and Austral Thrush accounted for 13, 12, 6.5, and 5%, respectively, of all individual birds counted in two point-count plots established around nest site A (RAFR unpubl. data). This may indicate that Chilean Hawks capture prey species in proportion to their local abundances; however, we could not test this possibility statistically because we studied only one nesting area. The Austral Thrush may have been captured preferentially because of its large body size (see Table 1). The White-crested Elaenia actively moves among branches when foraging, which may increase its detectability and, perhaps, its vulnerability to predation. It is not surprising that Chilean Hawks preyed on species inhabiting canopy or midstory layers because the hawks also occupy those layers; we were, however, surprised to find that these hawks also forage on ground-dwelling species (e.g., rhinocryptids). On most occasions, we observed Chilean Hawks moving with agility through and under the dense thickets of native bamboo inside the forest, thus demonstrating their ability to maneuver through dense habitats.

The diet of Chilean Hawks in our study area was very similar to that reported for the closely related Bicolored Hawk (*Accipiter bicolor*). In tropical forests of Guatemala, Thorstrom and Quixchán (2000) found that 95% of the identified prey delivered to nests was composed of birds, primarily passerines. Like the Chilean Hawk, the Bicolored Hawk in Guatemala ate rodents in small amounts (3%); in the Amazonian forest of Perú, Robinson (1994) reported at least 13 bird species and 1 squirrel species in the diet of Bicolored Hawks. In the southern temperate forest, the Chilean Hawk appears to take more birds than some other Falconiformes; for example, in a

Nothofagus forest of southern Chile, the diet composition of breeding Rufous-tailed Hawks (*Buteo ventralis*) was more evenly composed of birds and mammals (55 and 40%, respectively; Figueroa et al. 2000). In *Nothofagus* forests of southern Argentina, breeding White-throated Hawks (*B. albigula*) also had a more generalized diet, including not only birds but rodents and reptiles as well (Trejo et al. 2004). These comparisons, however, should be viewed with caution because each study entailed different methods of quantifying diet.

Increasing forest fragmentation in Patagonia may have detrimental effects on the diversity and composition of forest-dwelling species (Willson et al. 1994, Rau and Gantz 2001); in turn, this may have a negative effect on the availability of potential prey for forest-dwelling raptors. The Chilean Hawk should be given high priority in future studies to better understand its role and ecology in forest habitats.

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Short Communications

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Group Roosting Behavior of Yellow Tyrannulets (*Capsiempis flaveola*)

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ABSTRACT.—For 4 consecutive evenings in southern Nicaragua, a group of three Yellow Tyrannulets (*Capsiempis flaveola*) roosted in the same plant, and always arrived approximately 45 min before last light. Pre-roosting behavior appeared stereotyped and included mutual preening and a peculiar manner of hopping over one another. These three birds presumably left the roost around first light each morning. Received 4 May 2004, accepted 6 October 2004.

Despite the large amount of time birds spend at roost sites and their presumed vulnerability while asleep, little is known about roosting behavior of most species, especially those in the Neotropics. Skutch (1989) provides a general overview of avian roost sites and behavior, especially of Neotropical passerines. Among the Tyrannidae, Skutch (1989) reported “sleeping in contact” in both Platyrinchinae (Common Tody-Flycatcher, *Todirotum cinereum*) and Tyranninae (Social Flycatcher, *Myiozetetes similis*; Tropical Kingbird, *Tyrannus melancholicus*), whereas “sleeping in pairs” (i.e., roosting in close proximity, but not in contact) was noted in Tyranninae (Gray-capped Flycatcher, *Myiozetetes granadensis*; Boat-billed Flycatcher, *Megarhynchus pitangua*) and Elaeniinae (Yellow-bellied Elaenia, *Elaenia flavogaster*). In these examples, the roosting groups consist of a few individuals known or suspected to be paired or related. Cooperatively breeding birds may be particularly prone to roosting in contact (Skutch 1989), but few tyrannids are reported or suspected to breed cooperatively (2–3 species out of >375), and these species may not always do so (Thomas 1979, Ricklefs 1980, Brown 1987; J. A. Mobley pers. comm.). Migratory kingbirds (Tyranninae: *Tyrannus* spp.) have been observed roosting in large groups during the non-breeding sea-

son (Skutch 1989, Mayer 2004). Some tropical tyrannids that build covered or globular nests also roost (either individually or with young) in these structures year-round (Fluvicolinae: Sulphur-rumped Flycatcher, *Myiobius sulphureipygius*; Skutch 1989), and Eye-ringed Flatbills (Platyrinchinae: *Rhynchocyclus brevirostris*) sometimes build a different type of nest for roosting than for breeding (Skutch 1960). I describe here observations of the roosting behavior of a group of three Yellow Tyrannulets (Elaeniinae: *Capsiempis flaveola*), whose roosting behavior has not been described previously.

The Yellow Tyrannulet (7.9 g) is a sexually monomorphic, open-cup-nesting, lowland tyrannid, resident from eastern Nicaragua south across northern South America, and disjunctly(?) from Bolivia east into southeastern Brazil (Ridgely and Gwynne 1989, Ridgely and Tudor 1994, Hilty 2003). In Central America, it lives in pairs or small (possibly family) groups in lowland thickets, overgrown pastures, and forest edges (Skutch 1960, Ridgely and Gwynne 1989; SW pers. obs.), but is often associated with bamboo in South America (Ridgely and Tudor 1994; SW pers. obs.). The observations reported here were made in the evening, 6–9 April 2004, at the confluence of the Rio Bartola and Rio San Juan, Refugio Bartola, Depto. Rio San Juan, Nicaragua (10° 58' N, 84° 20' W; 30 m asl). Daytime temperatures were approximately 30° C, dropping to 22–25° C at night; there was no precipitation during this period. Observations were made at the edge of a clearing, where an overgrown pasture and secondary forest growth met. The 1.5-ha pasture was adjacent to the Rio San Juan, and consisted mostly of grasses (1.5–2 m high) interspersed with clumps (1.5–3 m high) of an unidentified slender, woody legume with finely pinnate leaves and yellow flowers.

On 6 April, at 17:40 CST (~15 min before sunset; 35 min before complete darkness),

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three Yellow Tyrannulets appeared, giving many single "wit" or "weet" notes. These vocalizations, while having a quality characteristic of the species, were unlike the typical two-syllabled calls given while foraging and at other times of the day. In contrast to the shy behavior of this species described by Skutch (1960), the birds were unwary, and gave no indication of being disturbed by my presence 15 m away. While making many short flights and hops through the vegetation, the group quickly converged on the roost plant, a thin woody legume (2.2 m high) entwined by a vine with cordate leaves. The birds all perched on the same branch 1.5 m above ground, which placed them at the lower edge of the plant's foliage. The birds' position left them completely exposed on three sides, but leaves from the plant and associated vine provided total cover from above—roost-site characteristics that Skutch (1989) reported for several other tyrannids.

Upon alighting on the roost branch, the birds appeared to "jockey" for position, frequently hopping over one another. This could have been an effort to gain the center position, but it was not uncommon for two birds to engage in this hopping while the third looked on from a branch a few centimeters away. This hopping behavior appeared highly stereotyped: a bird hopped over a single adjacent bird, and the hopping bird alit as close as possible to the bird it hopped over. Sometimes the hopping bird simply walked quickly over the back of its neighbor, but more typically the hopping was of the same character as that of the hopping exhibited by some male manakins (Pipridae) at leks. During this time, the birds frequently vocalized and faced opposite directions, but after 7 min they became silent and all faced the same direction. Once settled, the three birds were in direct contact with each other and the contour feathers were fluffed out somewhat. The birds remained in this position, eyes open and looking about, until total darkness. The most common position for the group entailed all birds facing the same direction, the middle bird looking straight ahead, and both outer birds looking away from the center one; this was the position the birds were in at the end of my observations on all 4 evenings. Roosting in direct contact with other individuals has been noted in both elac-

niine and tyrannine tyrannids, and most often involves young siblings, or young and their parents; adult mated pairs apparently roost less often in direct contact with each other (Skutch 1989).

During the next 3 evenings, the birds arrived slightly earlier (17:20–17:30), did not vocalize as much as on the first evening, and were always settled by 17:35. It was not possible to determine whether the birds always approached the roost site from the same direction or traveled together, but each evening they appeared synchronously from the vegetation surrounding the roost plant. A few sporadic observations of Yellow Tyrannulets in the pasture during the day were all of single individuals, but it was difficult to determine whether or not other individuals were nearby in thick vegetation. The birds always roosted in the same plant and alternated daily between roosting on one of two branches that were only a few centimeters apart. On one evening, after the birds had already settled, the birds were flushed from the roost by a pair of Grayish Saltators (*Saltator coerulescens*). The tyrannulets returned, briefly jockeyed for position, engaged in some mutual preening, and settled again within 4 min. Roost site fidelity in birds is not uncommon (Skutch 1989, Willis and Oniki 2003), but because I was only able to check the roost site for these 4 consecutive days, I do not know how frequently the site was used otherwise.

I was unable to determine precisely when the birds left the roost in the morning. On 2 mornings, I checked the roost at 05:30 (~25 min after first light) and the birds were already gone. I made one check of the roost at 04:30 (total darkness) with a flashlight, and the birds were still asleep at the roost. Thus, these birds probably left the roost somewhere around first light.

Despite observing the tyrannulets at close range with binoculars, I was unable to detect any differences in plumage or behavior that might suggest something about the relationship of the birds. Yellow Tyrannulets breed at almost any time of year (in Costa Rica) and lay two eggs per clutch (Skutch 1960); thus, it is not likely that this was a group of three young siblings roosting together, as Skutch (1989) describes for a group of Rusty-margined Flycatchers. Only the female is thought

to incubate eggs in Yellow Tyrannulets, but the male helps feed the nestlings (Skutch 1960). Extra-pair helpers at the nest are not known for Yellow Tyrannulets, and generally are rare among tyrannids (Brown 1987). Thus, I may have been observing two adults with one young, one adult with two young, or three adults. Either of the first two scenarios suggests that the young stay with their parents until their plumage appears (at least under field conditions) identical to that of the adult.

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Foraging by a Red-tailed Hawk along a Wetland Edge: How Large a Duck can be Captured?

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ABSTRACT.—A Red-tailed Hawk (*Buteo jamaicensis*; estimated mass 1,000–1,200 g) failed to kill a Red-breasted Merganser (*Mergus serrator*; estimated mass 1,150 g) that it captured in shallow water (<25 cm), but evidently dispatched a starving Red-necked Grebe (*Podiceps grisegena*; mass 645–660 g). These observations are pertinent to estimating the upper mass limit for successful foraging in water. Received 9 April 2004, accepted 2 September 2004.

Falconers were familiar with prey selection centuries before ideas about “optimal forag-

ing” were formalized (e.g., Krebs and Davies 1978). Originally, their interest was practical and involved questions such as what size prey a hawk could bring to the table. Much later, with the rise of wildlife management programs, raptor enthusiasts turned to broader ecological questions, including the impact and selective effects of predators on prey populations (e.g., Rudebeck 1950, 1951; Craighead and Craighead 1956; Luttich et al. 1970). In a classic study involving four species (*Accipiter nisus*, *Falco columbarius*, *F. peregrinus*, *Haliaeetus albicilla*), Rudebeck (1950, 1951) reported that an average of 19% (range: 14–33%) of birds captured for prey “exhibited injury, abnormality, or abnormal behavior.” From this he concluded that raptors probably selected weak or unfit birds in numbers dis-

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proportionate to their representation in the natural population. That viewpoint has become conventional wisdom (e.g., Mansell 1980) despite cautions that "the general idea that predators cull the injured and sick may be in part a phenomenon of what catches the human eye" (Drury 1998:163).

I report the behavior and prey choice of an immature Red-tailed Hawk (*Buteo jamaicensis*) that foraged in atypical habitat. Over the winter of 2002–2003, the hawk took up residence in a swampy woodland in Annapolis, Maryland, often perching 8 m high in a large oak (*Quercus* sp.) at the edge of a tidal, brackish water embayment. On 7 April 2003, at about 15:00 EDT on a cold (5°C) and rainy afternoon, the hawk jumped from its perch and plunged into the water about 30 m away. My initial view was obscured by vegetation, but much splashing ensued. Two min later I watched the soaked hawk struggle ashore with great difficulty, flapping its wings and hopping on one foot, the other being imbedded in the back of a still-living male Red-breasted Merganser (*Mergus serrator*; expected mass 1,150 g; Titman 1999). The strike had been made within 2 m of shore, probably in water <25 cm deep. After several minutes, the hawk dragged the merganser onto dry land and then stood over it for a few minutes, seemingly exhausted. It then "mantled" and attempted to finish the kill by severing the neck. But at the last minute the merganser struggled, like a wrestler avoiding being pinned, which nullified the effort. For the next 5 min, the hawk remained motionless, and then attempted the kill again with the same negative results. Once more it rested for 5–8 min, during which time the merganser occasionally ventured a weak flap, which elicited no response. The attempt to dispatch the merganser was repeated several more times, always ending in a stalemate. After 48 min, and with darkness approaching, the hawk suddenly gave up and flew away. The merganser lay motionless for about 30 sec, then shuffled into the water and swam out of sight, looking rumped and listing slightly to one side. At the site, I found no sign of blood and only a few merganser feathers.

Six days earlier I had found a dead, adult male Red-necked Grebe (*Podiceps grisegena*) 28 m from where the merganser was attacked; this was 60 m from the hawk's perch. The

grebe had been in the area for about 5 days previously, often diving in very shallow water within a few meters of shore. On examining the carcass, which was on shore and just above the high tide line, I judged that it had been dispatched by a raptor, and not scavenged by a mammal. The body had been ripped open from the back, the neck severed, and there were bill marks on the end of the scapula and ribs (cf. Blohm et al. 1980). The grebe was emaciated and, had it not been killed, would have soon died of starvation. Its gizzard contained a few well-ground fragments of beetle exoskeleton and two fresh amphipods about 7 mm long. The condition of the amphipods indicates that it had been capable of diving until a short time before its death and, therefore, had been killed. The carcass weighed 565 g and was lacking heart, lungs, part of the liver, and most of the intestine; part of the right breast and leg had been devoured. By extrapolating from data on the body composition of Eared Grebes (*P. nigricollis*; Jehl 1997) and comparing the mass of the intact and eaten parts of the Red-necked Grebe, I calculated that 90 g of muscle was missing and that the intact bird weighed 645–660 g. A healthy grebe in winter would be expected to weigh about 1,330 g (Stout and Nuechterlein 1999).

Red-tailed Hawks (average mass 1,000–1,200 g, depending on sex) feed mainly on small mammals, but have been known to take prey (e.g., jackrabbits) weighing up to about 2,000 g (Preston and Beane 1993). They have been reported occasionally (usually from prey found in the nest) to feed on several species of dabbling ducks, including Northern Pintail (*Anas acuta*; Bent 1937), and, in one instance, on a grebe (Luttich et al. 1970). In those reports, details of prey size, health, and the conditions of capture were not given. Sargeant et al. (1993) reported that certain raptors in the Prairie Pothole region may "prey extensively on adult ducks." Red-tailed Hawks were among the raptor species mentioned, but evidence for their involvement was circumstantial. Murphy (1994) observed a Red-tail feeding on an adult female Gadwall (*A. strepera*) in a prairie; the circumstances suggested that it had been caught on land nearby. He also saw an immature Red-tail capture a young Blue-winged Teal (*A. discors*) from a swim-

ming brood, and then transport it with great difficulty to shore. The average mass of pintails is 800 g (female) to 1,000 g (male; Austin and Miller 1995), mass of female Gadwalls is about 700 g (J. R. Jehl, Jr. unpubl. data), and that of teal ducklings is <400 g (Rowher et al. 2002).

A buteo's ability to capture and dispatch prey must be much greater on land than in water, where its normal killing behavior would be hampered. In the present case, a Red-tailed Hawk (1,000–1,200 g) failed to kill a Red-breasted Merganser (1,150 g) but killed a starving Red-necked Grebe (645–650 g). This suggests that the upper size limit for a Red-tailed Hawk to capture healthy prey in aquatic situations may be about 800 g. This is about 80% of its mass and approximately the average mass for large dabbling duck species. Additional observations would be instructive.

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Adult Gray Jay Captures an Adult Black-capped Chickadee

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ABSTRACT.—We observed an adult Gray Jay (*Perisoreus canadensis*) that had captured an adult Black-capped Chickadee (*Poecile atricapillus*) in Algonquin Provincial Park, Ontario, Canada, during winter. Aerial pursuit of small, adult birds and an instance of capture and predation of a juvenile bird by a Gray Jay have been reported previously. Here, we present the first documented case of capture of a seemingly uninjured, adult bird. Received 22 March 2004, accepted 12 October 2004.

The Gray Jay (*Perisoreus canadensis*) is well known for its diverse diet. Foods cited in the literature include arthropods, berries, carrion, nestling birds, fungi (Strickland and Ouellet 1993); a blood-stained weasel (Bent 1946); an injured Green-winged Teal (*Anas crecca*; Ouellet 1970); a well-decomposed seal carcass (Ouellet 1970); live deer mice (*Peromyscus maniculatus*; Gill 1974); blood-engorged winter ticks (*Dermacentor albipictus*; Addison et al. 1989); and insects caught in the air, flycatcher-style (Lawrence 1968, Strickland and Ouellet 1993). When available, eggs, nestlings, and weak-flying fledglings of many bird species are commonly eaten (Ouellet 1970, Strickland and Ouellet 1993).

It has been suggested that predation of adult birds by Gray Jays may be more regular than previously thought (Ouellet 1970, Barnard 1996). Here, we report the details of an adult Gray Jay that had captured an adult Black-capped Chickadee (*Poecile atricapillus*) during winter, which contributes to knowledge of the capture of independent vertebrate prey by Gray Jays.

On 26 February 2004, while birding along a road south of Lake Opeongo, Algonquin

Provincial Park, Nipissing District, Ontario, Canada (45° 37' N, 78° 21' W), our attention was drawn to a distress call that was loud, high-pitched, squeaky, and repeated quickly with few pauses. Upon turning toward the call, we were surprised to see a Gray Jay standing on top of a Black-capped Chickadee. The sound was given by the distressed chickadee as it attempted to escape the jay's grasp. One of the jay's feet appeared to be placed around the chickadee's neck, whereas the other foot grasped somewhere along the belly. We observed this act from about 10 m away, on a snow-covered, plowed roadway for approximately 5 sec, after which time the jay released the chickadee. The jay initially hopped away quickly and then flew off, while the chickadee, apparently unharmed, flew immediately to dense cover located 5 m away and disappeared. It is likely that the movement of a nearby photographer scared the jay. We suspect that if the jay had not been startled, it would have killed the chickadee.

Both the jay and the chickadee were probably initially attracted to seeds and bread that had been thrown along the plowed portion of the road. Two Gray Jays and up to a dozen Black-capped Chickadees had been visiting the road throughout the day, and during ~1 hr of watching the jays and chickadees earlier that same day, we did not witness any aggressive interactions, despite the fact that the birds fed within meters of each other. We did not observe the events prior to those described above; therefore, we do not know how the jay captured the chickadee.

The jay was uniquely color-banded, as part of a long-term study of Gray Jay nesting biology and behavior (see Strickland and Waite 2001), and belonged to a pair that was building a nest approximately 200 m from where the observation occurred. We observed this pair add material to their nest about 45 min before our observation, and we observed them again near the observation site a few minutes

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before the incident occurred. In the excitement of the moment, neither of us noted whether the jay standing on the chickadee was the male or the female.

Based on a comparison of the characteristics of the distress call that we heard given by the captured chickadee with the auditory descriptions of the major call types of chickadees outlined in the literature (Hailman 1989, Smith 1991), the call we heard was most similar to the "squeal" delivered by trapped adults of the Boreal Chickadee (*P. hudsonica*; Ficken et al. 1996), Mountain Chickadee (*P. gambeli*; McCallum et al. 1999), and Chestnut-backed Chickadee (*P. rufescens*; Dahlsten et al. 2002). Smith (1993) described squeals given by distressed, young Black-capped Chickadees soon after they fledge, but did not describe adult squeals. The duration of the noisy interaction we witnessed was likely too short (i.e., only about 5 sec) to attract attention from other birds; there have been reports of jay predation on birds during which distress calls lasting from 1 to 5 min elicited a mobbing response by nearby birds (Ehrlich and McLaughlin 1988, Curry 1990, Barnard 1996).

Barnard (1996) reported a juvenile Gray Jay that captured, killed, and consumed a juvenile Magnolia Warbler (*Dendroica magnolia*) that was capable of quick, sustained flight. This is the only previous report of an uninjured bird being captured by a Gray Jay (Barnard 1996). Strickland and Ouellet (1993) noted that small, adult birds are usually ignored by Gray Jays, although energetic, unsuccessful, aerial pursuits of Boreal Chickadees and Common Redpolls (*Carduelis flammea*) occasionally occur. Pike (1978) observed an adult Gray Jay capture an injured Black-capped Chickadee. The chickadee was already injured when it was found in a mist net—probably, the author explains, as a result of being pecked by a Gray Jay. When the chickadee was placed on the ground to recover, a Gray Jay grabbed it with its feet, and pecked on the chickadee's head several times before it flew off with it (Pike 1978).

Predation of adult or fledgling birds by other jay species has been reported elsewhere: Mourning Dove (*Zenaidura macroura*; DuBow 1985), Yellow-rumped Warbler (*Dendroica coronata*; Johnson and Johnson 1976). Purple

Finch (*Carpodacus purpureus*; Downs 1958), and House Sparrow (*Passer domesticus*; Master 1979) by Blue Jay (*Cyanocitta cristata*); Pygmy Nuthatch (*Sitta pygmaea*) and Dark-eyed Junco, gray-headed morph (*Junco hyemalis caniceps*) by Steller's Jay (*Cyanocitta stelleri*; Carothers et al. 1972); Northern Mockingbird (*Mimus polyglottos*) by Florida Scrub-Jay (*Aphelocoma coerulescens*; Curry 1990); European Starling (*Sturnus vulgaris*); Cliff Swallow (*Petrochelidon pyrrhonota*; Ehrlich and McLaughlin 1988), and Hermit Thrush (*Catharus guttatus*; McLandress and McLandress 1981) by Western Scrub-Jay (*Aphelocoma californica*); and an unknown sparrow by Mexican Jay (*Aphelocoma ultramarina*; Roth 1971). Use of the feet by jays to restrain avian prey, demonstrated by the Gray Jay in our observation, has been noted previously for Steller's Jay (Carothers et al. 1972), Blue Jay (Master 1979, DuBow 1985), Florida Scrub-Jay (Curry 1990), Western Scrub-Jay (Ehrlich and McLaughlin 1988), and Gray Jay (Pike 1978, Barnard 1996). By using their feet to restrain prey, the jays' bills are free to strike and kill their victims (McLandress and McLandress 1981, Ehrlich and McLaughlin 1988).

During periods of inclement weather in winter, some jay species appear to be attracted to small birds as a food source (Roth 1971, Carothers et al. 1972). The weather prior to and during our observation was not unusually harsh relative to average winter weather patterns for the area, suggesting this was not a contributing factor. Similarly, Johnson and Johnson (1976) and Master (1979) concluded that inclement weather was not a contributing factor to their observations of Blue Jay predation on birds. Inclement weather in winter should not influence Gray Jay predation on birds, given that this species relies on food cached throughout large, year-round, multi-purpose territories to survive harsh, boreal-forest winters (Strickland and Ouellet 1993). It is also highly unlikely that hunger was a motivating factor for this aggressive interaction because these jays were highly subsidized by artificial feeding, and they were demonstrating their superior nutritional state by nesting ahead of all other Algonquin Gray Jay pairs ($n = 20$) under observation at that time (R. D. Strickland pers. comm.).

Our observation, combined with observations by Barnard (1996) and Strickland and Ouellet (1993), suggest that Gray Jays capture small, adult passerines opportunistically throughout the year. This is the first documented instance of a seemingly uninjured adult bird being captured by a Gray Jay. These kinds of observations advance our understanding of interactions among species. Additional study is needed to reveal the frequency with which the Gray Jay preys on adult birds, and the environmental factors that influence this behavior.

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Flight Display Song of the Vermilion Flycatcher

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ABSTRACT.—A number of authors have qualitatively described the songs of Vermilion Flycatchers (*Pyrocephalus rubinus*) given during flight display, but no spectrograms or quantitative analyses are available. We present such a description based on displays of 14 different males. Our analysis confirms the impressions of earlier authors that the flight song is closely similar to that given by perched birds, but also revealed an important difference: most flight display songs also included an extra element known as the *peent* vocalization. The *peent* is also an alarm call, given during male-male and male-female interactions, as well as during foraging bouts. Besides reporting on the common use of *peent* vocalizations by perched Vermilion Flycatchers, we now describe the frequency and use of *peent* vocalizations in flight display songs. Received 4 March 2004, accepted 29 October 2004.

The repertoire of displays by the Vermilion Flycatcher (*Pyrocephalus rubinus*) includes a conspicuous flight display given during the breeding season (March to August, AARC pers. obs.). This display has been described (De Benedictis 1966, Smith 1967) and related to “territorial proclamation” (Smith 1970: 488). Anecdotal observations (AARC pers. obs.), where a male seems to respond with a flight display to a neighbor’s flight display, support the idea that individuals use this behavior in a male-male context. An interesting feature of flight displays is that they are accompanied by vocalizations. These vocalizations are considered to be closely related to the Regularly Repeated Vocalization, which is normally sung from a perch (Smith 1967, 1970). To add to our knowledge on the nature of songs uttered during flight displays, we present spectrograms of these songs ($n = 14$ males).

Our study was carried out in the Bosque de San Diego Metepec (19° 18' N, 98° 15' W),

Tlaxcala, México, from 6 March to 11 April 2001. Most observations and recordings were conducted from 08:00 to 11:00 or from 16:00 to 18:00, when birds were more active. Most males ($n = 11$) were banded and identified by their color-band combinations, whereas three males were identified by their choice of song post. Color-banded males typically used the same song perches; these perches were never used by other males, suggesting that the method for identifying unbanded males was appropriate. We mapped all territories and documented the number of neighbors for each male (mean = 2.57 ± 1.28 SD, range: 0–4). The territories were mapped by registering which perches were commonly used by males, noting male-male interactions (i.e., calling) that commonly occurred at territorial boundaries, and recording chases between territory owners and intruding males. A neighbor was defined as a male that had at least part of his territory adjacent to that of the focal male.

We recorded songs with a Sennheiser Me66 microphone and a Marantz PMD221 cassette recorder. Each male ($n = 14$) was recorded during one, 30-min period of observation. If the focal male had not performed a flight display within 30 min, we shifted to another focal male. This was done until all 14 males were recorded. All the males were paired, and although there were differences in the date each male was recorded, all 14 were recorded before their mates commenced nest construction.

Our sample size varied considerably between individuals (from 5 to 16 songs recorded per individual); however, we analyzed an equal number of songs per bird. We used either the whole sample (when $n = 5$ songs) or randomly selected five songs per individual (when $n > 5$ songs) resulting in a total of 70 songs analyzed. Songs were digitized on a PC computer using a sampling rate of 22,050 Hz. Songs were high-pass filtered with a cut-off frequency of 2.8 kHz. All variables were mea-

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TABLE 1. Song variation among male Vermilion Flycatchers was statistically significant for most parameters, but variation in the number of *peent* vocalizations was only marginally significant ($n = 14$ males). Data from recordings made at Bosque de San Diego Metepec, Tlaxcala, México, 6 March–11 April 2001.

Parameter	Mean \pm SD	Statistics: ANOVA or Kruskal-Wallis
Song duration (sec)	0.43 \pm 0.11	$H = 40.61$, $df = 13$, $P < 0.001$
Minimum frequency (kHz)	3.49 \pm 0.18	$F_{13,56} = 6.58$, $P < 0.001$
Maximum frequency (kHz)	5.97 \pm 0.21	$F_{13,56} = 7.80$, $P < 0.001$
Number of total elements	6.55 \pm 0.65	$H = 42.27$, $df = 13$, $P < 0.001$
Number of <i>peent</i> vocalizations	0.74 \pm 0.50	$H = 21.87$, $df = 13$, $P = 0.057$
Number of common elements	5.81 \pm 0.85	$H = 36.61$, $df = 13$, $P < 0.001$

sured on spectrograms calculated with AVISOFT (Specht 2002) software (FFT: 128; frequency resolution: 125 Hz; temporal resolution: 4 ms; window: Hamming). We measured song duration, minimum and maximum frequency, number of total song elements, number of *peents*, and number of common elements (Table 1). Means are presented \pm SD.

Flight display songs had the same basic structure and shared the same elements as the ones uttered while perched (Fig. 1A; Smith 1967). Elements found both in songs produced during flight displays and in songs uttered while perched are referred to as common elements. Songs had a mean of 6.55 elements \pm 0.65 (range: 5–8, $n = 70$), of which 5.81

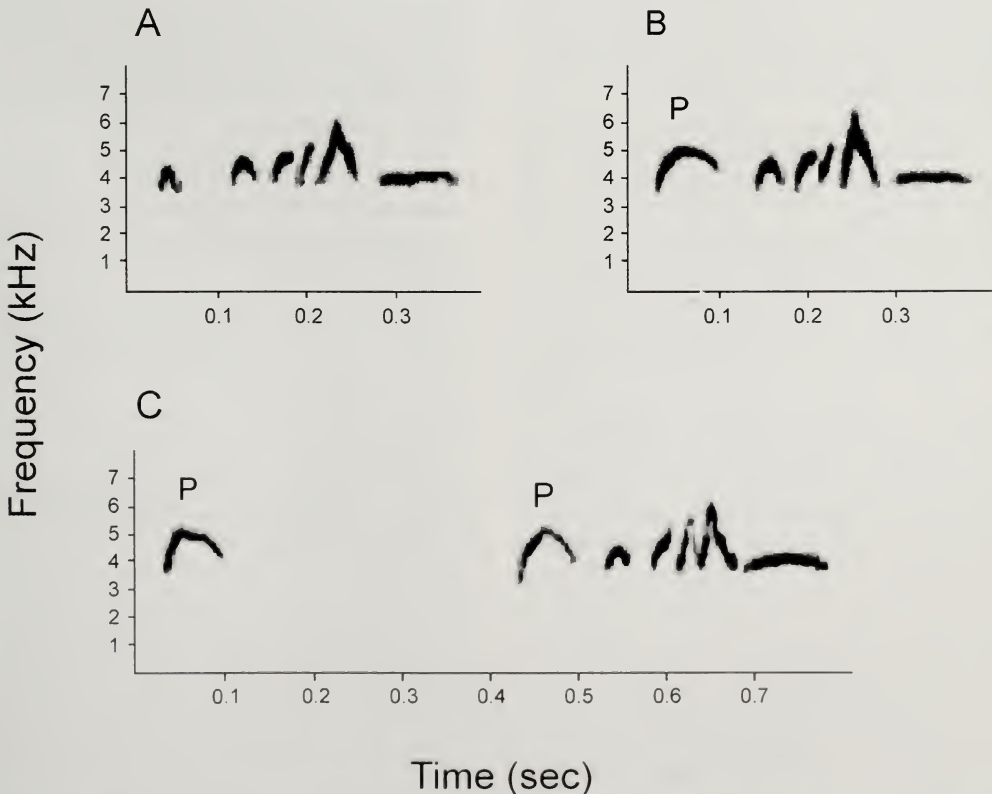


FIG. 1. Songs of Vermilion Flycatchers given during flight displays have a number of common elements (i.e., elements also found in songs given at a perch) and may include the *peent* vocalization. "A" represents a song with common elements. Spectrograms "B" and "C" represent songs that have one or two *peent* vocalizations (P). Recordings were made at Bosque de San Diego Metepec, Tlaxcala, México, 6 March–11 April 2001.

± 0.85 were common elements (range: 5–7, $n = 70$). Songs had a mean of 0.74 ± 0.50 *peent* vocalizations (range: 0–2, $n = 70$). In our study, 71.3% of the flight display songs had the *peent* vocalization; 68.5% had only one *peent* vocalization, 2.8% had two, and 28.7% lacked the *peent* vocalization. Songs lasted between 0.25 and 0.95 sec (mean = 0.43 ± 0.11), the minimum frequency ranged between 3.0 and 3.8 kHz (mean = 3.49 ± 0.18), and the maximum frequency ranged between 5.5 and 6.4 kHz (mean = 5.97 ± 0.21).

The *peent* vocalization has been previously described by Smith (1967; Fig. 1B, C) and is an alarm call, is given in male-male and male-female interactions, and when foraging (Smith 1967, Wolf and Jones 2000; AARC pers. obs.). As part of another study (AARC, CMG, and K. Riebel unpubl. data), we recorded songs of perched Vermilion Flycatchers given during the dawn chorus, and none of 119 songs included the *peent* vocalization. Thus, the *peent* does not constitute an element in songs of perched birds (AARC pers. obs.; see also Smith 1967).

All males sang at least one song with a *peent* vocalization; most individuals ($n = 13$) gave 0–1 *peents*. We found only one male that sang flight songs with a range of 1–2 *peent* vocalizations. Most males ($n = 8$) had either 5–6 ($n = 5$ males) or 6–7 ($n = 3$ males) common elements; four males had 5–7 ($n = 3$ males) or 6–8 ($n = 1$ male). All the songs of two males contained five common elements. Songs with a greater number of *peent* vocalizations had fewer common elements. We found a negative correlation between the number of common elements in a song and the number of *peent* vocalizations ($r = -0.60$, $P = 0.023$, $n = 14$), suggesting a trade off be-

tween these two groups of elements. We also found a negative correlation between the number of neighbors and the total number of elements in a song ($r = -0.63$, $P = 0.016$, $n = 14$), suggesting that different numbers of elements in songs may convey different messages to male Vermilion Flycatchers.

Finding a call (the *peent* vocalization) incorporated into a stereotyped song opens the question of whether this represents a variation in repertoire—whereby males modify song structure in different contexts. The relative importance of the *peent* vocalization and the number of elements in flight display songs in male-male and male-female communication must be addressed with playback experiments.

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Ornithological Literature

Edited by Mary Gustafson

WHY MUSEUMS MATTER: AVIAN ARCHIVES IN AN AGE OF EXTINCTION. Edited by Nigel J. Collar, Clemency T. Fisher, and Christopher J. Feare. Bulletin of the British Ornithologists' Club, vol. 123A—Supplement. 2003: 360 pp., 21 contributed papers (selected contributions at <http://www.boc-online.org/bulletin.htm#bul>). ISSN: 00071595, £22.00–24.00 (paper).—This volume stems from a meeting of the same name held in November 1999 in Tring. The meeting was the first of its type, and now is the first in a series, meant to bring members of the European avian collections community together in an effort to enhance international cooperation among museum biologists. In the New World, we have the annual meetings of the American Ornithologists' Union and the list serve AVECOL (established by J. Van Remsen, Jr.) that seem to promote a degree of interaction that had not yet been achieved among European institutions. The breadth of participants (130 people from 25 countries) and authors (36 people from 13 countries, many outside of Europe) demonstrates a success that reaches well beyond Europe.

This is a dynamic time to be a museum biologist—although the title of this volume reflects some of the community's angst—as we continue an inexorable transition from the description of avian diversity and distribution to a more diverse array of scientific pursuits. The collection of papers in this volume is rather eclectic, which is to be expected given the great diversity of materials that museums preserve and the variety of ways in which these materials are used in avian research.

The bulk of the volume treats traditional collections of skins, skeletons, fluid specimens, eggs, and associated paper (labels, catalogues, journals, etc.). DNA, proteins, tissue collections, databases (Christidis and Norman, Rajkowski), and sound collections (Alström and Ranft) are also included, as are two chapters on the electronic amalgamation of museum data (Peterson et al. and Navarro et al.).

The highlight of the volume is C. S. Ro-

selaar's *An Inventory of Major European Bird Collections*, which, at 85 pages, is the longest contribution. He summarizes 109 larger collections (the A-list) in some detail, and another 151 are listed in much less detail (the B-list: collections of <4,000 skins, or <5,000 bird items, or institutions that did not return the questionnaire that served as the basis for his paper). A long reference section and three appendices provide additional details that make this heterogeneous assemblage of collections accessible to researchers everywhere. I consider the data presented in Roselaar's chapter to be the hallmark of the meeting; the paper coalesces the collaborative, broad interest of museum biologists and is a summary of lasting value to collections-based ornithology.

Those eager to see data from museum labels made available electronically and to use these data in analyses will do well to read Rasmussen and Prÿs-Jones' paper *History vs Mystery: The Reliability of Museum Specimen Data*. Museum collections generally contain rich and accurate data, but there are many ways in which data quality is compromised, and museum personnel are accustomed to uncovering errors using clues such as specimens and handwriting that are unavailable electronically.

Collar and Rudyanto, in *The Archive and the Ark: Bird Specimen Data in Conservation Status Assessment*, demonstrate how important museum specimens can be in conservation (Peterson et al. and Navarro et al. extend this notion for Mexico). They also point to the decline in the number of specimen-based taxonomists and systematists (important in their case at the "twig" level) as being detrimental to conservation. Collar and Rudyanto's paper is important both for conservation biologists and museum administrators. The authors see molecular studies growing at the expense of more traditional studies in taxonomy and systematics, and suggest that this emphasis has begun to "marginalize specimen collections in the eyes both of space-stressed administrators pondering their budgets and of result-oriented

academics planning their immortality.” The authors recognize that the complementarity between these areas of study is important; however, I would go further and suggest that specimen-based science itself is changing. There is much important, traditional, avian taxonomic work to be done, but such studies are no longer viewed as being central in the reward structures of scientific institutions: it is expensive work, for which it is very difficult to receive grant support, and it is not publishable in top journals. Many of those who continue to pursue traditional taxonomy do so because they love it and recognize its importance—despite annual performance metrics that often focus on grant dollars brought in, journal impact factors, and citation rates. This is a situation that requires attention, and perhaps a partial solution is that of cross-appointments between conservation organizations and museums.

There are many excellent reasons why all museums should forge stronger ties with library archives and link specimens to associated paperwork in an accessible manner. Fisher and Warr, in *Museums on Paper: Library and Manuscript Resources*, provide a series of well-illustrated examples regarding the importance of being able to access the paperwork associated with museum specimens. In *Egg and Skin Collections as a Resource for Long-term Ecological Studies*, Green and Scharlemann provide a good, brief survey of nontraditional uses for traditional specimens.

For all of its successes, I feel that the volume overall is not adequately forward-looking. For example, reasons for continued growth of collections (and there are many) are expressed in fewer than half the contributions (e.g., Olson, Livezey, Christidis and Norman, Green and Scharlemann, Kitchener and McGowan). Reinvigoration of collection-based ornithology throughout Europe will require active, vibrant collections that continue to grow and become available for, and relevant to, a changing array of research questions. The final contribution—a summary of post-meeting workshops by Cooper and Steinhilber—shows that the future of avian collections is tremendously important to the meeting participants; however, their brief summary of the most dynamic areas in this

business make it clear that it is just a first step and that more is needed.

This volume will help the museum community and its increasingly diverse clientele understand some of the positive and negative aspects of past and present specimen-based ornithology—and in some cases it outlines directions for the future. There is not an adequate summary of the dynamic landscape of museum biology, however. An introductory overview would have helped to summarize the diverse messages that the symposium authors provide and would have given more cohesion to the whole volume. The lack of an overview, however, does not detract from the volume’s successes, particularly insofar as the symposium establishes a new forum for continued meetings and discussions among members of the European avian collections community. But if these meetings and symposia are to be effective in changing extrinsic factors impinging upon specimen-based ornithology, reaching out beyond our community is imperative. This volume is a good beginning.—KEVIN WINKER, University of Alaska Museum, Fairbanks, Alaska; e-mail: ffwksw@uaf.edu

ECOLOGY AND CONSERVATION OF BIRDS OF THE SALTON SINK: AN ENDANGERED ECOSYSTEM. Edited by W. David Shuford and Kathy C. Molina. *Studies in Avian Biology* No. 27. Cooper Ornithological Society, Camarillo, California. 2004: 169 pp., 43 figures, 42 tables, 9 pen-and-ink sketches, 8 maps, 8 black-and-white photographs, 7 color photographs. ISBN: 1891276379, \$17.00 (paper).—This book is an organized collection of scientific articles assembled together in a single volume, the objectives of which are to present baseline biological/ecological data on the Salton Sea’s avifauna and elucidate the long-term perspective of these works; emphasize the importance of the Salton Trough to avian populations; and describe the Salton Sea’s connectivity with the Colorado River Delta and Pacific Flyway. Although there are no chapter headings, the articles can be generally classified into three sections—ecological and historical perspectives, species assemblages, and species-spe-

cific issues—with introductory and closing articles provided by the editors. The target audience of this book should have a scientific interest and background in avian ecology or ecosystem management. However, most articles are not so technical as to be beyond the understanding of readers with a more general interest in these topics. The literature cited for each article is compiled in a reference section at the end of the volume, which increases readability for non-scientific readers.

The articles dealing with historical and ecological perspectives provide the reader with a background on natural ecological processes and more recent anthropogenic changes that have shaped avian use of the Salton Sea. Several authors document the historic and dynamic hydrological connection between natural Colorado River flows to the Salton Trough and the current agricultural flows that sustain the static elevation of the modern Salton Sea. The effects of land-use change are linked to the makeup of avian assemblages found in the region. The history of avian discoveries is also traced in this section, notably the first documentation of the western race of Gull-billed Tern (*Sterna nilotica vanrossemi*) in 1927 and the first regional record of Large-billed Savannah Sparrow (*Passerculus sandwichensis rostratus*) in 1930.

The bulk of the book is dedicated to articles on species assemblages, their use of the Salton Sea and lower Colorado River Delta, and associated upland and riparian habitats. Habitat use, species abundance, and importance of the Salton Trough to shorebirds, colonially nesting waterbirds, Neotropical migrants, seabirds, and waterfowl are all described. Most landbirds have a Sonoran Desert affinity, whereas waterbirds are associated with the Colorado River and coastal California. As Shuford et al. note, “. . . the Salton Sea has a rich shorebird fauna that rivals or exceeds that of most sites in western North America.” For Neotropical migrants, Flannery et al. suggest that the Salton Trough is in the main-stream portion of the flyway rather than along the periphery, and that the area is an important stopover where migrants may replenish fat reserves in an otherwise desert region. More than 400 avian species have been recorded in the Salton Trough; Orange-crowned Warbler (*Vermivora celata*), Audubon's Warbler (*Den-*

droica coronata auduboni), Wilson's Warbler (*Wilsonia pusilla*), Yellow Warbler (*D. petechia*), and Warbling Vireo (*Vireo gilvus*) are all listed as key species.

Articles contained within the species-specific issues section express a diversity of perspectives. They range from documenting habitat use and the high numbers and densities of Burrowing Owls (*Athene cunicularia*) in the Imperial Valley to identifying potential and probable causes for the substantial disease outbreaks that have occurred in pelican and grebe populations at the Salton Sea. Several authors indicate that agricultural practices have led to the largest and most densely populated area of Burrowing Owls in California. Rocke et al. note that the 1996 botulism outbreak was the first recognition that type C avian botulism was considered a major threat to pelican populations; in that event, an estimated 15% of the western population of American White Pelicans (*Pelecanus erythrorhynchos*) was lost. Similarly, Meteyer et al. document and describe a mostly undiagnosed cause for the loss of an estimated 6% of the North American population of Eared Grebes (*Podiceps nigricollis*) in 1991–1992.

This book provides data and descriptions for the many superlative “firsts” and “mosts,” both positive and negative, attributed to the Salton Sea. All authors agree and point to the connectivity with lower Colorado River Delta resources. Most recognize that contaminants and lack of adequate water flows affect the entire ecosystem, including the Delta and Gulf of California. As stated in the introductory article, this book meets its stated objectives of providing baseline data, identifying the importance of the avian resources, and demonstrating connectivity between the Salton Trough and the lower Colorado River Delta.

The editors leave us with a summary of the threats and issues facing the Salton Sea today and into the future. Water diversions and agricultural and urban development have led to declines in habitat in the Salton Trough and Colorado River Delta regions. Salination, eutrophication, contamination, exotics, disease, disturbance, and the threat of a large-scale water transfer also threaten resources. The need for bi-national management and conservation planning to restore habitat is identified, as is

current interest in the Salton Sea's biota, and recreational and economic development. The authors provide the reader with a glimpse of what may happen if we let the system go instead of engineering a solution to the problems facing the Salton Sea and Colorado River Delta. Finally, the editors challenge readers to get involved, not necessarily at a scientific level, but with socio-political issues that impact the Salton Sea and its associated resources.

The scientific format of this publication is not intended for the casual birdwatcher or reader with a general interest in natural science. It is recommended for the avid birdwatcher and ornithologist who wishes for a more complete understanding of the reasons and importance of why a species or group of species uses a given geographic area. However, it is also highly recommended for the student or scientist of conservation biology, ecosystem management, desert avifauna, and ecology of the Salton Trough and Colorado River Delta ecosystem.—CHARLES PELIZZA, Hawaiian and Remote Pacific Islands National Wildlife Refuge Complex, Honolulu, Hawaii; e-mail: charlie_pelizza@fws.gov

THE TOS HANDBOOK OF TEXAS BIRDS. By Mark W. Lockwood and Brush Freeman. Texas A&M University Press, College Station. 261 pp., 140 color photos, 627 maps, 4 appendices. ISBN: 1585442836, \$50.00 (cloth). ISBN: 1585442844, \$24.95 (paper).—Perhaps no other state enjoys as much attention from birdwatchers as does the state of Texas. Each year, thousands, probably tens of thousands, of birders from out of state visit Texas in search of the wide variety of bird species that occur there—species from both eastern and western North America, and those that can be found only in southern Texas. Roger Tory Peterson proclaimed on numerous occasions that the state bird list for Texas was much greater than for any other state. Indeed, he even wrote his own field guide dedicated to Texas. The truth is somewhat more complex. This fourth edition of the TOS (Texas Ornithological Society) "Checklist" includes 623 species—impressive indeed, but California's list is within just one or two species of that total. Comparisons be-

tween the two state lists are difficult because the TOS accepts for its main list only species documented by photograph or specimen, whereas the California Bird Records Committee accepts sight-only records (3–4 species). Which state is actually "ahead" in the number of species depends upon the criterion used. Texas has five species on its 'Presumptive' list (acceptable sight-only records).

The book opens with short introductory sections on Texas ornithological history, topography, and climate. The bulk of the book consists of the species accounts, which include concise information on status. For every species there is a range map, which in a general way accurately reflects the status of every species, even casual and accidental species (for which the records are represented by dots). This is certainly the most valuable part of the book, and although I have not read every account, they seem to accurately portray the distribution of Texas birds. Nonetheless, I might quibble over a few points. For instance, the accounts of eastern *Empidonax* species do not indicate that all of those species—except Acadian Flycatcher (*Empidonax virescens*)—are circum-Gulf migrants, and are therefore rare to casual on the Upper Texas Coast, particularly in spring. Louisiana birders who see almost exclusively only Acadian Flycatchers in spring know this. I wondered just how well-documented the winter reports of Common Nighthawk (*Chordeiles minor*) were, a species that winters only in South America. Lesser Nighthawk (*Chordeiles acutipennis*) would seem to be a much more likely winter resident. Only species accepted by the Texas Birds Records Committee (TBRC) are included and I fully approve of that treatment. A few of the species though—White-chinned Petrel (*Procellaria aequinoctialis*), Dark-billed Cuckoo (*Coccyzus melacoryphus*), and Black Catbird (*Melanoptila glabrirostris*)—have not been accepted by either the American Birding Association Checklist Committee and/or the American Ornithologists' Union Committee on Classification and Nomenclature. While I do not fault the authors for following the TBRC, the contrary opinions of other respected groups should have been mentioned. The origin of the Black Catbird specimen seems particularly dubious. One could also question the validity (on grounds of origin) of White-

checked Pintail (*Anas bahamensis*) and Blue Mockingbird (*Melanotis caerulescens*), and the photos of the Yellow-footed Gull (*Larus livens*) do not look especially convincing (viewed separately in *Texas Birds*). But, every state probably has a few records of species that are never adequately resolved.

As useful as the species accounts are, they are somewhat incomplete in that there is not enough detail about the timing of bird movements. Yes, a general time frame is provided (e.g., late March to mid-April, late August to mid-October), but I would prefer details on the earliest and latest records, when the first slight pulse of migrants normally occurs, when a species' migration peaks, etc.). Only then can an observer thoroughly learn a species' distribution and realize the significance of his or her own sighting, especially when there is a need to carefully document sightings that fall well outside the expected range of dates. Perhaps these data do not exist for Texas. If this is the case, there should be an effort to begin such a compilation and establish a database. Texas is a huge state and this task will be difficult. Still, many other states have such information and this is reflected in a number of well-done books on state birds. Bruce Peterjohn's book, *The Birds of Ohio*, is a particularly good example of a work that covers all of this in great detail and should be a primer for all potential authors contemplating works of status and distribution.

The species accounts include some information on subspecies, but overall I felt that much more could have been done. For instance, which subspecies did the Pine Grosbeak (*Pinicola enucleator*) specimen represent? Readers will need to turn to the third edition of the *Checklist of the Birds of Texas* (1995) or to the two-volume *Bird Life of Texas* by Harry Oberholser (1974) for that information.

Perhaps the most valuable part of the book is the 140 well-reproduced color photos that document numerous rarities, many of which are casual or accidental species to Texas and/or North America. The authors and the publisher are to be commended for publishing this archival information. However, a major shortcoming is that the date and exact locality information are not given for every photo.

The book is dedicated to Greg Lasley, who, as Secretary of the TBRC, invigorated the or-

ganization, and—while serving for many years as a Regional Editor (along with his co-editor Chuck Sexton)—did everything he could to get documentation for the records submitted for publication to *North American Birds* and its predecessors. His efforts were not always appreciated. For decades in Texas, one's word was good enough in establishing an exceptional record of occurrence. It is a Texas tradition perhaps, but makes for very bad science. Sincere people can be wrong in their identifications, and when researchers go back and try to verify exceptional records, the fact that so-and-so was a well-respected birder just is not good enough. I admire the authors for dedicating their book to Greg. When you see Greg or Chuck in the field please thank them for their accomplishments in greatly advancing Texas ornithology.

In conclusion, this book makes available to the general public a concise work on the birds of Texas. It should be owned by not only every Texas birder, but by every other birder in North America. If you haven't visited Texas to birdwatch, it is only a matter of time until you do.—JON L. DUNN, WINGS, Bishop, California; e-mail: cerwa@earthlink.net

BIRDLIFE OF THE CHURCHILL REGION: STATUS, HISTORY, BIOLOGY. By Joseph R. Jehl Jr., illustrated by the author. Trafford Publishing, Victoria, British Columbia, Canada. 2004: 154 pp., 8 color and 10 black-and-white plates, 4 maps, 2 figures, 2 tables, 30 sidebars. ISBN: 1412031079, \$28.00 (paper).—This book elaborates on and updates *Birds of the Churchill Region, Manitoba* (1970) by Jehl and Blanche A. Smith. The text incorporates a rigorous examination of pertinent documentation, including a profusion of historical anecdotal material. It is a culmination of previous attempts to describe the Churchill avifauna. Throughout the book, the author's familiarity with the birds of the Churchill region is immensely evident and his qualifications in that regard add indisputable credence to his assertions with respect to occurrences and abundances of species.

The book is structured to reflect the author's perspectives based on his personal ornithological research in the region, which spans four

decades, and incorporates valuable data and comments of other researchers who collectively have studied many of the 285 bird species confirmed locally. Preparation of the text clearly involved consultation with many sources, and the historical information presented adds valuable insight regarding the former status and distribution of birds.

A brief ornithological history of the Churchill region, with a focus on the considerable contributions of Samuel Hearne (ca. 1780), precedes a discussion of the local topography and geology. Information on local human population fluctuations, economic development, environmental considerations, and climate trends augment the historical account.

The rich and extensive texts of individual species accounts stress the distinctiveness of the local avifauna. The accounts focus on breeding and (where applicable) migration chronologies, nesting ecologies, prominent behaviors, and documented occurrences. The author's own personal observations attractively embellish some accounts of avian displays and other important breeding activities. Some species, by virtue of their local prominence, are treated more thoroughly than others. Special emphasis is placed on Lesser Snow Geese (*Chen c. caerulescens*) that breed at La Perouse Bay, and pertinent ongoing research initiatives there are instructively outlined in accompanying sidebars. Distributional changes of Ross's Goose (*C. rossii*) in northern Manitoba are described. Canada Geese (*Branta canadensis*) receive special focus because of the recent and dramatic growth in their local population and a long history of research on Canada Geese in the region.

Detailed accounts are given for several species that have been studied locally with varying degrees of thoroughness: Long-tailed Duck (*Clangula hyemalis*), Semipalmated Plover (*Charadrius semipalmatus*), Whimbrel (*Numenius phaeopus*), Hudsonian Godwit (*Limosa haemastica*), Semipalmated Sandpiper (*Calidris pusilla*), Dunlin (*C. alpina*), Stilt Sandpiper (*C. himantopus*), Short-billed Dowitcher (*Limnodromus griseus*), Red-necked Phalarope (*Phalaropus lobatus*), Yellow Warbler (*Dendroica petechia*), Blackpoll Warbler (*D. striata*), Lapland Longspur (*Calcarius lapponicus*), and Smith's Longspur (*C. pictus*). Speculative rationale is given for recent,

local declines in breeding-populations of some species, notably Lapland Longspur and Semipalmated Plover.

The exhaustive literature cited section comprises over 270 references. Illustrative Christmas Bird Count data and avian clutch sizes for the Churchill region are presented in two closing tables. Abundant description, teeming with detail, renders this book an important contribution to the ornithological literature and a major resource that furthers the understanding of avifauna in the Churchill region. The historical data are particularly helpful in structuring a comprehensive impression of the dynamics of interspecific relationships. Periodic references to dramatic local population declines and redistributions are insightful, but nonetheless somewhat unsettling. The long duration of many avian research programs in the Churchill region affords a rather unique opportunity to examine local avian ecological transformations, and to relate these developments to climate change and landscape alteration resulting from local human activities.

A table of contents would have been useful, but in view of the comprehensiveness of the text, I found it a rather inoffensive omission. The absence of an index is somewhat of an inconvenience. Nonetheless, my overall impression of the book is that of a rigorous, professional, and unpretentious examination of fundamental information on status, history, and biology of the Churchill region's avifauna, presented in a comprehensive and instructive manner. Reading the book is enjoyable and enormously rewarding. Highly recommended.—ROBERT M. ALISON, Orilla, Ontario; e-mail: hifsus@hotmail.com

HANDBOOK OF THE BIRDS OF THE WORLD, VOLUME 8: BROADBILLS TO TAPACULOS. Edited by Josep del Hoyo, Andrew Elliott, and David Christie. Lynx Edicions, Barcelona, Spain. 2003: 845 pp., 81 color plates, over 470 color photographs, 672 maps. ISBN: 8487334504, \$195.00 (cloth).—Volume 8 marks the commencement of the Passeriformes, almost a second beginning for this landmark series. A Foreword on the history of avian taxonomy by Murray Bruce leads off the book, starting in ancient Greece and

continuing to today. This tome contains information about a wide variety of families: members of the brightly colored Eurylaimidae (broadbills), Philepittidae (asites), and Pittidae (pittas) contrast with members of the more subdued Furnariidae (ovenbirds), Dendrocolaptidae (woodcreepers), Thamnophilidae (typical antbirds), Formicariidae (ground-antbirds), Conopophagidae (gnateaters), and Rhinocryptidae (tapaculos). The format of volume 8 is much the same as it was in earlier volumes in the series, as one would expect. The treatment for each taxonomic family begins with a brief overview, highlighted in a green box, that includes a brief family description, the range of body sizes, geographical distributions, habitats, and the number of taxa in the family—including those that are threatened or extinct. A more complete discussion of the family immediately follows in text, with sections on systematics, morphological aspects, habitat, general habits, voice, food and feeding, breeding, movements, relationships with man, and status and conservation.

Liberally illustrated with color photographs, every two-page spread contains one or more stunning images that portray a wide range of family members and behaviors. Generally, the photos are very sharp, large in size, and full of life—not static, stiff portraits, but images of behavior, foraging, nest building, nests, and bathing. Some are comical, such as that of the Black-and-red Broadbill (*Cymbirhynchus macrorhynchus*) facing the camera with beak agape; others are stunning portraits, including those of the Black-and-yellow Broadbill (*Eurylaimus ochromalus*) and Garnet Pitta (*Pitta granatina*). Even rare or recently (re)discovered species, such as Gurney's Pitta (*Pitta gurneyi*), are included. Nest photographs include one of a male Scalloped Antbird (*Myrmeciza ruficauda*) on the nest (but seemingly more buried in the leaf litter). On every page, birds are sleeping, bathing, sunning, feeding, or nesting—and one Blackish Cinclodes (*Cinclodes arcticus*) is confronting face-to-face what appears to be a southern elephant seal (*Mirounga leonina*). Many species in these families are skulkers and difficult to see, much less capture on film in artistically composed photographs while displaying interesting behaviors. This is a truly remarkable collection of images.

The plates are simple in design, with a solid background and the birds are depicted on natural vegetation or without perches (the woodcreepers). The work of several artists is represented, with most families illustrated by a single artist throughout. The sole exception is the tapaculos, illustrated by two artists. The standard of the artwork in the plates is very high and the end result pleasing. Many subspecies are illustrated where appropriate. The plate illustrating the Whiskered Pitta (*Pitta kochi*) and Red-bellied Pitta (*Pitta erythrogaster*) has 12 full-bodied portrayals and 8 head or head-and-shoulders illustrations.

The family descriptions are followed by the species accounts, in which portions of the family overview are repeated with more specific information on habitat, food habits, feeding, breeding, movements, and status and conservation. Each account begins with a color plate followed by the text for that species. This format makes the book much easier to use than it would be if the color plates were disjunct from their associated text. Subspecies are illustrated for many species and are described briefly in the text. Each account provides a range map, a list of the species' common names in various languages, old names used for the taxon, and a summary of the species' taxonomy. Subspecies' authorities, geographic location of occurrence, and descriptive notes are provided—including vocal descriptions. A bibliography concludes each account.

Improvements in volume 8 are just tweaks of the series' proven formula. For example, the base maps now show major rivers, and the photo captions contain the English names of birds in boldface type to make it easier to locate the species' name in the sometimes lengthy captions. A reference list of recordings is now included, and the reference list of Scientific Descriptions now includes the number of the page on which each taxon is described. Because many of these families are poorly known, the editors note that more unpublished information is referenced.

For those not fortunate enough to have started with volume 1, volume 8 represents a chance to begin with the passerines. Wherever you start, this is a landmark series and I highly recommended it.—MARY GUSTAFSON, USGS Patuxent Wildlife Research Center, Laurel, Maryland; e-mail: mary_gustafson@usgs.gov

PROCEEDINGS OF THE EIGHTY-FIFTH ANNUAL MEETING

SARA R. MORRIS, SECRETARY

The eighty-fifth annual meeting of the Wilson Ornithological Society was held Thursday, 22 April, through Sunday, 25 April 2004, in Ithaca, New York, in joint session with the Association of Field Ornithologists. The meeting was hosted by the Cornell Laboratory of Ornithology. Scott Sutcliffe chaired the local committee, which also included Linda Minde, Diane Tessaglia-Hymes, Phyllis Dague, and many members of the Cornell Lab of Ornithology staff.

The Council met from 13:00 to 17:15 on Thursday, 22 April, in the Fuertes Room of the Johnson Center for Birds and Biodiversity at the Cornell Laboratory of Ornithology. That evening there was a wine and cheese reception for conferees in the Morgens Observatory at the Johnson Center. Members of the Cayuga Bird Club led early morning bird walks at Sapsucker Woods.

On Friday, 23 April, Scott Sutcliffe, Chair of the Local Committee and President of the Association of Field Ornithologists, welcomed guests to the Multipurpose Room of the Appel Commons on the Cornell University campus. After his announcements about recent bird sightings and other local information, Doris Watt made several additional announcements about student awards. Charles Blem, President of the Wilson Ornithological Society, welcomed conferees and thanked the local committee. Scott Sutcliffe introduced Jed Burt, who provided background on Margaret Morse Nice and introduced Steve Emlen of Cornell University, who presented the eighth annual Margaret Morse Nice Plenary Lecture, "Birds 'R' Us: Chronicles of an Avian Anthropologist." Two concurrent paper sessions were presented in the Auditorium and the Multipurpose Room of the Robert Purcell Union throughout the remainder of the scientific program. In addition to the Nice lecture, the scientific program included 59 contributed papers, organized into eight paper sessions, and 46 contributed posters.

On Friday evening, conferees were invited to a reception, an informal dinner, and tours at the Johnson Center for Birds and Biodiversity. John Fitzpatrick, the Louis Agassiz Fuertes Director of the Cornell Laboratory of Ornithology, welcomed conferees to the inaugural year celebration of the new lab. Director Fitzpatrick provided some background about the Johnson Center, indicating that the new lab was built to interpret and conserve the earth's biological diversity and, specifically, as a temple to the magic of birds.

Participants spent the morning of Saturday, 24 April, on field trips to Dryden Lake and surrounding areas, Montezuma National Wildlife Refuge, and Summerhill and the surrounding area including the Finger Lakes Land Trust's Dorothy McIlroy Bird Sanctuary. Saturday evening began with a cocktail hour among the posters in the First Floor Conference Room at the Rob-

ert Purcell Union. The reception and poster session were followed by a joint members' meeting for both societies in the Auditorium of the Purcell Union.

The annual banquet was hosted in the Trillium of Kennedy Hall. After the dinner, Scott Sutcliffe recapped the meeting and introduced Cecilia Riley, who announced the AFO student awards. President Blem then briefly addressed the conferees, thanked Scott for hosting the meeting, the members of the Cayuga Bird Club for their service, and the Scientific Program Committee for a successful meeting. He thanked the retiring Members of Council for their service, welcomed the new Members of Council, and thanked all committee members for their hard work. At that time the awards and commendations that follow were presented by Leann Blem (Travel Awards and Student Research Awards), John Smallwood (Edward's Prize), Jed Burt (Margaret Morse Nice Medal), and Doris Watt (Student Presentation Awards). The meeting was adjourned by acclamation at 21:02.

MARGARET MORSE NICE MEDAL (for the WOS plenary lecture)

Dr. Stephen Emlen, "Birds 'R' Us: Chronicles of an Avian Anthropologist."

EDWARD'S PRIZE (for the best major article in volume 115 of *The Wilson Bulletin*)

Julie C. Hagelin, "A field study of ornaments, body size, and mating behavior of the Gambel's Quail." *Wilson Bulletin* 115(3):246–257.

LOUIS AGASSIZ FUERTES AWARD

Stéphanie M. Doucet, Auburn University, "Female choice and sexual ornamentation in lekking Long-tailed Manakins, *Chiroxiphia linearis*: do females choose good genes?"

GEORGE A. HALL/ HAROLD F. MAYFIELD AWARD (formerly the Margaret Morse Nice Award)

Felicity Newell, Chatham College, "Comparison of success and habitat for the Wood Thrush and American Robin in southwestern Pennsylvania."

PAUL A. STEWART AWARDS

Shannon N. Bouton, University of Michigan, "The effect of multiple environmental stressors on the

physiology, behavior and development of nestling Cliff Swallows."

Courtney Murdock, University of Michigan, "Resource levels, parasite load, and reproduction in a wild population of Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) in western Colorado."

Dustin R. Rubenstein, Cornell University, "Sexual conflict and extrapair paternity in the plural cooperatively breeding Superb Starling, *Lamprolaima superbus*."

Laura Henderson Spinney, Princeton University, "Hormonal mediation of alternative phenotypes in the White-throated Sparrow (*Zonotrichia albicollis*)."

WILSON ORNITHOLOGICAL SOCIETY TRAVEL AWARDS

Jeremy E. Guinn, North Dakota State University, "Bald Eagle nesting habitat use and responses to human presence in Minnesota."

Emily Morse, Penn State Erie, "The roles of rank, state, and seasonal considerations on foraging behavior in Black-capped Chickadees."

Valeria Ojeda, Universidad Nacional del Comahue, Argentina, "Breeding behavior of Magellanic Woodpeckers (*Campephilus magellanicus*) in Argentine Patagonia."

Michael Shepard, University of Wyoming, "Situation-specific call use in Leach's Storm-Petrel (*Oceanodroma leucorhoa*)."

Vinodkumar Saranathan, Ohio Wesleyan University, "Effect of solar ultra-violet radiation on feather-degrading bacteria."

Amy Schneider, Ohio Wesleyan University, "Does a shift in preen wax composition have antibacterial implications for breeding sandpipers?"

ALEXANDER WILSON PRIZE

(for the best student paper)

Dana M. Hawley, Cornell University, "The price of the pecking order: how dominance status mediates immunity in wintering House Finches (*Carduelis mexicanus*)."

LYNDS JONES PRIZE

(for the best student poster)

Rebecca Heiss, Binghamton University, "Mouth color and tail shape as an indicator of age in American Crows."

BEST UNDERGRADUATE PAPER AWARD

(for the best student paper or poster by an undergraduate)

Megan M. Szymanski, Cornell Lab of Ornithology, "High lineage diversity and host sharing of malarial parasites in a local avian assemblage."

Selection committee for the Nice Medal—William E. Davis, Jr. (Chair), Charles Blem, James Rising, and Doris Watt; for the Edwards Prize—John Smallwood (chair), Karl Miller, and Doris Watt; for the Fuyes, Hall/Mayfield, and Stewart Awards—Leann Blem (chair), Charles Blem, Clait Braun, Dale Gawlik, Dale Kennedy, Dan Klem, David Podlesak, Craig Rudolph, and Doug White; for the Wilson Ornithological Society Travel Awards—Leann Blem (chair); and for the Student Presentation Awards—Doris Watt (chair), Curt Adkisson, Bob Beason, Arla Hile, and Bridget J. M. Stutchbury.

BUSINESS MEETING

President Charles Blem called the business meeting to order at 18:09 in the Auditorium of the Purcell Union at Cornell University. He thanked Scott Sutcliffe for hosting the meeting.

Secretary Morris summarized the Council meeting of Thursday, 22 April. As of 31 March 2004, the Wilson membership stood at 1,857 including 163 students. The Wilson membership represents 39 countries. We also have 72 library subscriptions to *The Wilson Bulletin*. As part of the OSNA report, Council learned of several Wilson members who had died since the Society last met, and Secretary Morris asked assembled members to stand while she read the following names: Walter J. Breckenridge (Minneapolis, MN), W. H. Carrick (Toronto, ON, Canada), Svein Haftorn (Klaebu, Norway), Wayne C. Harris (Swift Current, SK, Canada), Ed N. Harrison (Camarillo, CA), Ned K. Johnson (Berkeley, CA), Vincent C. Jones (Chevy Chase, MD), Henry C. Kyllingstad (New London, MN), Roxie C. Laybourne (Manassas, VA), Daniel L. Leedy (Silver Spring, MD), Gordon C. Sauer (Kansas City, MO), Sally F. H. Spofford (Portal, AZ), and Alice E. Ulrich (Niagara-on-the-Lake, ON, Canada).

During the past year, the WOS received the William and Nancy Klamm bequest and hired Howland Capital Management to manage the assets from their estate. The distributions that were received from this estate have more than doubled the Society's assets. To comply with new accounting standards, the Society has chosen to have more than one person overseeing the financial operations, and thus the Council agreed to outsource accounting services. Furthermore, Council changed the Investing Trustees Committee to the Finance/Audit/Investment Committee that will include the Board of Trustees, the President, and the Treasurer. This committee will address potential conflicts of interest, investment policies, and other matters relating to the finances of the Society.

The Council reelected Jim Sedgwick as editor of *The Wilson Bulletin* for Volume 117. Council substantially increased the support of the editorial office, with the understanding that this increase would result in the publication of all four issues of volume 116 this calendar year, and thus get the journal back on publication schedule and continue the enhancement of the quality of the journal.

Council heard an update on the 2005 meeting, which

will be hosted by the USGS Patuxent Wildlife Research Center and the Maryland Ornithological Society. The meeting will be in conjunction with the Association of Field Ornithologists and will be held 21–24 April in either Bowie or Laurel, Maryland. Council agreed to participate fully in the 2006 NAOC (North American Ornithological Conference). There may be interest in having another smaller meeting in that same year.

Martha Vaughan presented the Treasurer's Report and Jim Sedgwick presented the Editor's Report.

Jerry Jackson presented the report of the Nominating Committee, which included William E. Davis, Jr., Danny J. Ingold, and Bette J. S. Jackson. The committee recommended the following slate of candidates: President, Charles R. Blem; First Vice-President, Doris J. Watt; Second Vice-President, James D. Rising; Secretary, Sara R. Morris; Treasurer, Martha Vaughan; and Members of Council, Albert R. Buckelew (2004–2005), Timothy O'Connell (2004–2006), Robert Curry (2004–2007), Mary Bomberger Brown (2004–2007), and Jamie Hill (2004–2007). President Blem thanked the nominating committee and asked for any nominations from the floor. Hearing none, he accepted a motion to close nominations by John Kricher, seconded by Jed Burt. Chan Robbins moved that the Secretary cast a single ballot for the nominees, and Jed Burt seconded the motion. Secretary Morris cast the ballot, electing the officers and council members.

President Blem adjourned the meeting at 18:21 after a motion from Jerry Jackson, which Doris Watt seconded.

COMMENDATION

WHEREAS the Wilson Ornithological Society and the Association of Field Ornithologists helped celebrate the inaugural year of the Johnson Center by holding their annual meetings in Ithaca, New York, at Cornell University's Laboratory of Ornithology; and

RECOGNIZING that the Scientific Program Committee, consisting of Ted Davis, Ricky Dunn, Eduardo Iñigo-Elias, Linda Minde, Laura Stenzler, Jim Rising, Ken Rosenberg, and Scott Sutcliffe, provided an extensive and varied program of oral and poster presentations; and

RECOGNIZING that the Committee on Local Arrangements, chaired by Scott Sutcliffe with extensive assistance by Linda Minde, arranged conference venues at the Cornell Laboratory of Ornithology and on the Cornell University main campus that fostered opportunities to attend a variety of presentations, to experience the many roles of the Laboratory of Ornithology, including some in surround sound, and to enjoy numerous avian and culinary delights;

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society and the Association of Field Ornithologists commend the Scientific Program Committee, the Committee on Local Arrangements, especially Scott Sutcliffe and Linda Minde, and all others who helped to make this meeting at Cornell University a resounding success, and one that will serve as a benchmark for future meetings.

REPORT OF THE TREASURER

OPERATING BUDGET FOR FISCAL YEAR 2004
Amended and Approved at Annual Meeting, 22 April 2004

	Budget 2003	Actual 2003	Budget 2004
Operating Revenue			
Direct Public Support (Contributions)	1,500	1,193.00	1,200
Memberships	32,000	45,816.00	46,000
Subscriptions	23,000	16,616.00	17,000
Page Charges	13,000	11,696.00	12,000
Royalties	1,000	1,689.66	1,600
BioOne Electronic Licensing	5,100	5,181.09	6,632
Sale of Back Issues & Books (Van Tyne Library)	1,000	1,107.10	1,000
Interest Income—Cash Accounts	1,000	116.89	0
Total Operating Revenue	77,600	83,415.74	85,432
Operating Expenses			
Research Grants and Awards	8,000	6,000.00	6,000
Student Travel Grants	2,000	1,530.00	5,000
Van Tyne Library—Student Salaries/Benefits	1,500	6,197.35	2,000
Printing/Mailing Costs— <i>Wilson Bulletin</i> (Allen Press)	80,000	42,306.03	70,750
Editor's Honorarium, Contract, Expenses (Vol. 115)	20,000	9,035.87	595
Editor's Honorarium, Contract, Expenses (Vol. 116)	10,000	8,099.04	55,000
OSNA Management Services	13,000	16,083.50	17,000
OSNA Executive Director	3,000	3,857.00	4,000
Storage Costs—Back Issues	550	2,064.70	2,000
Membership Development	1,500	1,971.00	1,500
Support—American Bird Conservancy	150	150.00	150
Support—Ornithological Council	3,000	9,000.00	9,000
Support—Ornithological Council Retreat	0	0.00	1,000
Tax Preparation Fees	600	525.00	525
Accounting Services	0	0.00	5,500
Insurance Expenses	1,000	1,090.00	1,150
General Expenses—Office, Postage, Copying, Bank Charges	1,500	631.74	1,000
Travel Expenses—Ornithological Council, OSNA, NABC Annual Meetings	5,000	1,772.99	2,500
Van Tyne Library Expenses	1,500	992.48	1,000
Award Costs	1,000	750.00	800
Total Operating Expenses	153,300	112,056.70	186,470
Excess (Deficit)—Operating	(75,700)	(28,640.96)	(101,038)
Total Investment Income	55,500	146,706.21	65,340
Excess (Deficit) Including Investments	(20,200)	118,065.25	(35,698)
Invested Bequest—Klamm Estate: Howland Capital Management	0	1,233,084.12	0
Total Excess (Deficit) Including Klamm Bequest	(20,200)	1,351,149.37	(35,698)

STATEMENT OF ACTIVITIES

FISCAL YEAR ENDING 31 DECEMBER 2003

Operating Revenue	Actual
Direct Public Support (Contributions)	\$ 1,193.00
Memberships	45,816.00
Subscriptions	16,616.00
Page Charges	11,696.00
Royalties	1,689.66
BioOne Electronic Licensing	5,181.09
Sale of Back Issues & Books (Van Tyne Library)	1,107.10
Interest Income—Cash Accounts	116.89
Total Operating Revenue	83,415.74
Operating Expenses	
Program Services	
Research Grants and Awards	\$ 6,000.00
Student Travel Grants	1,530.00
Van Tyne Library—Student Salaries/Benefits	6,197.35
Printing/Mailing Costs— <i>Wilson Bulletin</i> (Allen Press)	42,306.03
Editorial Expenses (Vol. 115)	9,035.87
Editorial Expenses (Vol. 116)	8,099.04
OSNA Management Services	16,083.50
OSNA Executive Director	3,857.00
Storage Costs—Back Issues	2,064.70
Membership Development	1,971.00
Support—American Bird Conservancy	150.00
Support—Ornithological Council	9,000.00
Total Program Services (95%)	\$ 106,294.49
Support Services	
Tax Preparation Fees	\$ 525.00
Insurance Expenses	1,090.00
General Expenses—Office, Postage, Copying, Bank Charges	631.74
Travel Expenses—Ornithological Council, OSNA, NABC Annual Meetings	1,772.99
Van Tyne Library Expenses	992.48
Award Costs	750.00
Total Support Services (5%)	\$ 5,762.21
Total Operating Expenses	\$ 112,056.70
Excess (Deficit)—Operating	\$ (28,640.96)
Investments (Including Sutton Fund)	
Realized Gain/Loss on Investments	\$ 37,845.32
Unrealized Gain/Loss on Investments	84,299.73
Investment Income—Dividends/Interest	25,863.50
Investment Fees/Taxes	(1,302.34)
Total Investment Income	\$ 146,706.21
Total Excess (Deficit) Including Investments	\$ 118,065.25
Invested Bequest—Klamm Estate: Howland Capital Management	
Bequest Distributions (Cash and Equities)	\$ 1,157,130.28
Realized Gain/Loss on Investments	(52,982.68)
Unrealized Gain/Loss in Investments	122,012.76
Investment Income—Dividends/Interest	10,873.23
Investment Fees/Taxes	(3,949.47)
Total Income—Klamm Bequest	\$ 1,233,084.12
Total Excess (Deficit) Including Klamm Bequest	\$ 1,351,149.37

STATEMENT OF FINANCIAL POSITION

FISCAL YEAR ENDING 31 DECEMBER 2003

Assets

Current Cash Assets

Merrill Lynch—Operating Cash	\$ 77,437.00	
Comerica Checking—Van Tyne Account	684.40	
University of Michigan—Van Tyne Account	149.53	
Merrill Lynch—Cash Equivalents—Investments	19,658.58	
Sutton Fund—Merrill Lynch—Cash Equivalents	986.52	
Howland Management—Cash Equivalents	89,033.50	
Total Current Cash Assets		\$ 187,949.53

Investments

Merrill Lynch—Equities	\$ 606,390.00	
Merrill Lynch—Corporate Bonds	126,968.00	
Merrill Lynch—Mutual Funds	25,548.00	
Sutton Fund—Merrill Lynch—Equities	118,620.00	
Sutton Fund—Merrill Lynch—Corporate Bonds	9,904.00	
Howland Management—Equities	881,296.94	
Howland Management—Fixed Income	262,753.68	
Total Investments		\$ 2,031,480.62
Total Assets		\$ 2,219,430.15

Fund Balances

Fund Balances—Beginning of Fiscal Year

Operating Cash Accounts	\$ 106,911.89	
Investments—Merrill Lynch	655,985.00	
Sutton Fund—Merrill Lynch	105,383.89	
Klamm Fund—Howland Capital Management	0.00	
Total Fund Balances—Beginning of Year		\$ 868,280.78

Current Year Change in Fund Balances

Operating Cash Accounts	\$ (28,640.96)	
Investments—Merrill Lynch	122,579.58	
Sutton Fund—Merrill Lynch	24,126.63	
Klamm Fund—Howland Capital Management	1,233,084.12	
Total Current Year Change		\$ 1,351,149.37

Fund Balances—End of Fiscal Year

Operating Cash Accounts	\$ 78,270.93	
Investments—Merrill Lynch	778,564.58	
Sutton Fund—Merrill Lynch	129,510.52	
Klamm Fund—Howland Capital Management	1,233,084.12	
Total Fund Balances		\$ 2,219,430.15

Martha Vaughan, *Treasurer*

EDITOR'S REPORT—2003

At the annual meeting of the Wilson Ornithological Society (March 2003), I was elected to succeed retiring John Smallwood as Editor of *The Wilson Bulletin*, beginning with volume 116 (1), March 2004. I received my first batch of manuscripts from Editor Smallwood on 8 September 2003. The editorial office was established at the USGS Fort Collins Science Center in Fort Collins, Colorado, during the summer and two editorial assistants have been hired, one full-time and one half-time.

A total of 130 manuscripts was received during 2003, 10 fewer than in 2002 and 45 fewer than in

2001. Outgoing Editor Smallwood handled the first 61 manuscripts and I processed the remainder (69). I have accepted 27% and rejected 29% of manuscripts received in 2003, with the rest (44%) having been returned to authors for extensive revision or revision and re-review. The mean time from receipt to initial decision for manuscripts received at the new Editorial Office in 2003 was 108 days. The time from receipt to final acceptance for papers (to be) published in 116(1) was 188 days [*Auk*: 317 days (vol. 120); *Condor*: 233 days (vol. 105)]. We continue the trend of increased electronic correspondence and manuscript transmission begun in Editor Blem's term.

I greatly appreciate the assistance of John Small-

wood for his advice and encouragement throughout the transition period. I am grateful to Clait Braun, Richard Conner, Kathleen Beal, and Karl Miller who served on the Editorial Board and reviewed numerous manuscripts. Kathy Beal gave expert statistical critiques of several manuscripts. Editorial assistants Beth Dillon and Cynthia Melcher performed essential editorial office operations including setting up an e-mail correspondence tracking system, revising and maintaining the author/manuscript database, corresponding with authors and reviewers, copy editing, and consulting with Allen Press and other editors. I thank Allen Press for guidance and helpful advice on the final stages of the editorial process. The USGS Fort Collins Science Center has been instrumental in the establishment and support of the new editorial office. We welcome suggestions on how to improve the timeliness and quality of *The Wilson Bulletin*.

James A. Sedgwick, *Editor*

The reports of the standing committees are as follows:

REPORT OF THE MEMBERSHIP COMMITTEE

Current members of the WOS membership committee are Jim Ingold, Louisiana State University, Chair (LA); John Smallwood, Montclair State University (NJ); and Robert Sargent, Robins AFB, (GA).

Membership of Committee: We could use two additional active participants. Any suggestions on how we could gather new input are welcome, as well as how we can contact the complete membership of the society.

The new WOS poster was displayed at the WOS meeting in Ohio. Mistakes were discovered and the display was out of commission until they were fixed. The renovated display will be shown at the meeting at Cornell.

The membership chair regularly receives inquiries from members regarding the journal and the status of their membership. Most of these are received via e-mail. The rate of messages has increased with journal lateness.

Jim Ingold, *Chair*

REPORT OF THE JOSSELYN VAN TYNE MEMORIAL LIBRARY COMMITTEE

I am very pleased to submit this report of the activities at the Josselyn Van Tyne Memorial Library. The following happened over the past calendar year with respect to the library:

Loans:

Loans of library materials to members included 80 transactions to 39 members. These loans included 6 books and 390 photocopied articles.

Acquisition of volumes:

Exchanges: A total of 148 publications was received by exchange from 114 organizations or individuals.

Gifts: We received 30 publications from 25 organizations.

Subscriptions: We also received 35 publications from 29 subscriptions. We spent a total of \$585.52 on subscriptions in 2003.

Donations: Members, friends, and libraries donated 477 items. These donations included 3 books, 354 journal issues, 72 reprints, and 48 reports.

Donors: The five members, friends, and libraries donating materials include Norbert Bahr, Charles Collins, Harold Hanson (via Tex Sordahl), The Peregrine Fund, and Jeffrey Spendelow.

Purchases: New items purchased for \$210.42 included 3 books, 1 pamphlet, and 10 journal volumes.

Dispersal of volumes:

Gifts to Other Institutions: A total of 124 journal issues was donated to the Hawk Mountain Sanctuary library, 24 back issues of *The Wilson Bulletin* to Norbert Bahr, 116 journal issues were donated to Point Reyes Conservation Science library, and 1 book was donated to Dr. E. O. Willis at UNESP in Brazil.

Back Issues: We sent out 285 back issues of *The Wilson Bulletin* for only the cost of postage.

Duplicates: We sold 15 duplicate books and 53 duplicate journal issues for \$577.00.

Events:

Downsizing Storage: Our storage area for back issues of *The Wilson Bulletin* was changed last summer. We now have room to store only about 50 to 75 copies of each issue. We found ourselves overstocked on many issues, so before the move we disposed of and recycled many back issues, keeping a maximum of around 50 to 75 copies of each. We did not discover, until after the disposal, that Bridge to Asia (www.bridge.org), a charity run out of Chicago and San Francisco, will accept English language books and journals. All we need to do is get them to Chicago and they will send them on to libraries in need in Asia. If someone cannot drop off our donated materials in the future, then perhaps we can advertise in OSNA for donations to cover the postage.

Accessibility on the Web:

Web site: The Web site (<http://www.ummz.lsa.umich.edu/birds/wos.html>) continues to provide access to the library. Journals currently received are listed on the site as well as how to access the University of Michigan's online catalogue, which interested people can use to check holdings.

Books for Sale: We have our duplicate books for sale listed on the Web site.

Journals for Trade: Also listed on the Web are the journals we have available for sale or trade.

Hellos, Good Byes, and Thank You:

We hired a new secretary, Janet Bell, to replace Mary Jo Nemeth, who was our temporary secretary for two years. We want to express our thanks to Mary Jo and say a hearty welcome to Janet Bell.

My most heart-felt thank you goes to 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 who is incredibly helpful to members and friends wanting to use the library. Janet not only makes my job quite easy, she makes my job possible.

Terry L. Root, *Chair*

REPORT OF THE UNDERGRADUATE OUTREACH COMMITTEE

This WOS Committee continues to maintain the Guide to Graduate Programs in Ornithology on the WOS Web site. Occasional e-mails from users indicate the guide is a valuable resource for students contemplating graduate study in ornithology.

Herb Wilson, *Chair*

The Committee on the Scientific Program, which included William E. Davis, Jr., Erica Dunn, Eduardo Inigo-Elias, Linda Minde, Laura Stenzler, James Rising, Ken Rosenberg, and Scott Sutcliffe, presented the following program of paper and poster sessions.

PAPER SESSIONS

John Anderson, College of the Atlantic, Bar Harbor, ME; Alan Mainwaring, Robert Szewczyk, and David Culler, University of California at Berkeley, Berkeley, CA, "Microhabitat monitoring in Leach's Storm-Petrels."

David R. Barber and Keith L. Bildstein, Hawk Mountain Sanctuary, Kempton, PA, "Patterns in the geographic range sizes of New World Falconiformes."

David Bonter, Cornell Lab of Ornithology, Ithaca, NY; and Elizabeth W. Brooks, Braddock Bay Bird Observatory, Rochester, NY, "Are elevated mist nets required to adequately sample the avian community at a migration stopover site?"

Kimberly S. Bostwick, Cornell University, Ithaca, NY, "High-speed video of wing-sound production in two species of manakins (Aves: Pipridae)."

Patricia L. R. Brennan, Cornell University, Ithaca, NY, "Home range of male and female Great Tinamous in a lowland tropical forest."

John N. Brzorad, Forsyth College, Winston-Salem, NC; Alan D. Maccarone, Friends University, Wichita, KS; and Kevin J. Conley, Forsyth College, Winston-Salem, NC, "Foraging energetics of Great and Snowy Egrets during the breeding season."

Anne B. Clark, Binghamton University, Binghamton, NY; Kevin J. McGowan, Cornell Lab of Ornithology, Ithaca, NY; Douglas A. Robinson, Jr., and Rebecca Serrell, Binghamton University, Binghamton, NY, "Patterns of mortality from West Nile Virus in a marked population of American Crows in Ithaca, Tompkins Co., New York, 2002-2003."

William S. Clark, Harlingen, TX, "Wave molt of the primaries in Accipitrid raptors, and its use in ageing immatures."

William S. Clark, Harlingen, TX; and Christopher C. Witt, Louisiana State University, Baton Rouge, LA, "First known specimen of a hybrid *Buteo*: Swainson's Hawk X Rough-legged Hawk from Louisiana."

John Confer, Ithaca College, Ithaca, NY, "A shrub is not just a little bush: a review."

Caren B. Cooper and Harold Mills, Cornell Lab of Ornithology, Ithaca, NY, "The sound of incubation rhythms and bluebirds."

Kimberly Corwin, NYS DEC, Albany, NY; and Valerie Freer, Atlas Steering Committee, Ellenville, NY, "New York State's second Breeding Bird Atlas."

John Dunning, Jr., Alexandra Houston, Kathryn Lester, and Dan Scheiman, Purdue University, West Lafayette, IN, "Hoosier National Forest bird population trends: preliminary analyses."

Cristina R. Faustino and Evan G. Cooch, Cornell University, Ithaca, NY, "Mycoplasmal conjunctivitis in wild House Finches: population structure, movement, and seasonal disease dynamics."

Peter T. Fauth, Hartwick College, Oneonta, NY, "Short-term demography of the Veery in south-central New York."

Carol R. Foss and Pamela D. Hunt, Audubon Society of New Hampshire, Concord, NH, "Avian community patterns in a northern New England urbanizing landscape."

Margaret S. Friar, University at Albany, Albany, NY; and Ian C. T. Nisbet, I. C. T. Nisbet & Co., North Falmouth, MA, "Adoption in Common Terns: benefits to the donor brood."

Jeremy E. Guinn and James W. Grier, North Dakota State University, Fargo, ND; Joan Galli and Richard J. Baker, MN DNR, St. Paul, MN; and Jody G. Milar, U.S. Fish and Wildlife Service, Rock Island, IL, "Bald Eagle nesting habitat use and responses to human presence in Minnesota."

Meena Haribal and André Dhondt, Cornell Lab of Ornithology, Ithaca, NY; and David Rosane and Eloy Rodriguez, Cornell University, Ithaca, NY, "Chemical compositions of preen gland secretions of passerines: same goal achieved by different means."

Dana M. Hawley, Cornell University, Ithaca, NY, "The price of the pecking order: how dominance status mediates immunity in wintering House Finches (*Carpodacus mexicanus*)."

James R. Hill, III, Purple Martin Conservation Association, Edinboro, PA; Scott A. Rush and Bridget J. M. Stutchbury, York University, Toronto, ON, Canada, "The influence of acid rain on the productivity of Purple Martins: a continent-wide, multi-year perspective."

David J. T. Hussell, Ontario Ministry of Natural Resources, Peterborough, ON, Canada, "Tactics for coping with a variable environment: laying interruptions and extended incubation in Tree Swallows."

Eduardo E. Inigo-Elias, Cornell Lab of Ornithology, Ithaca, NY, "Trade of Neotropical migratory passerine birds: conservation implications across nations."

- Eduardo E. Inigo-Elias, Cornell Lab of Ornithology, Ithaca NY; Humberto Berlanga, Comision Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), D.F., Mexico; Hector Gomez de Silva Garza, UNAM, D.F., Mexico; and Arvind Panjabi, Rocky Mountain Bird Observatory, Brighton, CO, "Species conservation assessment in Mexico: national and continental priorities."
- Frode Jacobsen, Lutz Bachmann, and Jan T. Lifjeld, University of Oslo, Oslo, Norway; and Marit Nesje, The Norwegian School of Veterinary Science, Oslo, Norway, "The effects of severe population bottlenecks and a reintroduction project on the genetic diversity of south Scandinavian Peregrine Falcons (*Falco peregrinus*)."
- Christopher S. Jennelle and Evan G. Cooch, Cornell University, Ithaca, NY, "The importance of incorporating encounter probabilities in estimates of disease prevalence: an example using the House Finch-*Mycoplasma gallisepticum* system."
- Sara A. Kaiser and Catherine A. Lindell, Michigan State University, East Lansing, MI, "Effect of proximity to forest edges on nestling growth and nest survival of Wood Thrush in southwestern Michigan."
- James S. Kellam, Ithaca College, Ithaca, NY, "Predation risk, starvation risk, and radio transmitters in Downy Woodpeckers."
- E. Dale Kennedy, Katherine Niesen, and Douglas W. White, Albion College, Albion, MI, "Individual variation in songs of House Wrens."
- Stephen W. Kress and C. Scott Hall, National Audubon Society, Ithaca, NY, "Thirty years of puffin restoration on the Maine coast, USA."
- Jacob E. Kubel and Richard H. Yahner, The Pennsylvania State University, University Park, PA, "Nesting ecology of the Golden-winged Warbler in three early successional habitats of central Pennsylvania."
- J. Daniel Lambert and Kent P. McFarland, Vermont Institute of Natural Science, Woodstock, VT, "Potential effects of climate change on Bicknell's Thrush habitat in the northeastern United States."
- Paulo E. Llambías, Cornell University, Ithaca, NY, "Differences in social mating system and parental care between Northern House Wren (*Troglodytes aedon*) and Southern House Wren (*T. musculus*)."
- Michael P. Lombardo, Michelle L. Green, Patrick A. Thorpe, Grand Valley State University, Allendale, MI; and Matthew R. Czarnowski, Rutgers University, New Brunswick, NJ, "Repeated sampling affects Tree Swallow semen characteristics."
- Irby J. Lovette, Cornell Lab of Ornithology, Ithaca, NY, "Redefining *Wilsonia* and other unnatural groups of wood-warblers."
- Alan D. Maccarone, Friends University, Wichita, KS; and John N. Brzorad, Forsyth College, Winston-Salem, NC, "Foraging behavior of Great and Snowy Egrets in relation to prey availability."
- John N. Mager, Cornell University, Ithaca, NY, "Experimental analysis of the behavioral consequences of using nest platforms for management of Common Loons (*Gavia immer*)."
- Kevin J. McGowan, Cornell Lab of Ornithology, Ithaca, NY; Anne B. Clark and Douglas A. Robinson, Jr., Binghamton University, Binghamton, NY; and Carolee Caffrey, Audubon Science, Ivyland, PA, "Familial care-giving in American Crows."
- Alexander M. Mills, University of Toronto, Toronto, ON, Canada, "Can habitat be sexually rather than ecologically prescribed?"
- Alexander M. Mills, University of Toronto, Toronto, ON, Canada, "Spring and autumn migration timing changes in North American migrant passerines during a period of global warming."
- Emily Morse and Margaret Voss, Penn State Erie, The Behrend College, Erie, PA, "The roles of rank, state, and seasonal considerations on foraging behavior in Black-capped Chickadees."
- Timothy J. O'Connell, Oklahoma State University, Stillwater, OK; Michael L. Lanzzone and Robert S. Mulvihill, Powdermill Nature Reserve, Rector, PA; Daniel W. Brauning, Pennsylvania Game Commission, Harrisburg, PA; and Duane Diefenbach, Penn State University, University Park, PA, "How well do removal models applied to count data estimate known densities from territory mapping?"
- Valeria Ojeda, Universidad Nacional del Comahue, Bariloche, Argentina, "Breeding behavior of Magellanic Woodpeckers (*Campephilus magellanicus*) in Argentine Patagonia."
- Gail L. Patricelli, Marc S. Dantzker, and Jack W. Bradbury, Cornell Lab of Ornithology, Ithaca, NY, "Directionality in acoustic communication: a field study on Red-winged Blackbirds."
- Terrell D. Rich, U.S. Fish and Wildlife Service, Boise, ID; David J. Krueper, U.S. Fish and Wildlife Service, Albuquerque, NM; and Jonathan Bart, USGS-BRD, Boise, ID, "Comparison of spring and fall bird population trends following the removal of cattle from the San Pedro River, Arizona."
- Kenneth Roblee, Bureau of Wildlife, Buffalo, NY; Ward Stone, Wildlife Pathology Unit, Delmar, NY; and David Adams, Nongame and Habitat Unit, Albany, NY, "Type E botulism caused waterbird mortality in the New York waters of Lake Erie and Lake Ontario, 2000-2003."
- Rebecca J. Safran, Cornell University, Ithaca, NY; Kevin J. McGraw, University of California-Davis; Matthew R. Evans, University of Exeter in Cornwall, United Kingdom; and Colby Rice Neuman, Cornell University, Ithaca, NY, "Geographic differences in the function of sexual ornaments: plumage coloration, not tail-streamers, is a sexually selected trait in North American Barn Swallows."
- César Sánchez, Branko Hilje, Rodolfo Jaffé, and Gilbert Barrantes, Universidad de Costa Rica, San José, Costa Rica, "Vocal variation in the Green Violetear, a Neotropical hummingbird."
- Vinodkumar Saranathan and Edward H. Burt, Jr., Ohio Wesleyan University, Delaware, OH, "Effect

- of solar ultra-violet radiation on feather-degrading bacteria.”
- Amy Schneider and Edward H. Burt, Jr., Ohio Wesleyan University, Delaware, OH; and Jeroen Reenkerens, Royal Netherlands Institute for Sea Research, Den Hoorn, The Netherlands, “Does a shift in preen wax composition have antibacterial implications for breeding sandpipers?”
- Edwin Scholes, III, Yale University, New Haven, CT, “Courtship repertoire of Carola’s Parotia in Papua New Guinea: a video-based ethological analysis.”
- Michael A. Shepard, Starksboro, VT, “Situation-specific call use in Leach’s Storm-Petrel (*Oceanodroma leucorhoa*).”
- W. Gregory Shriver and James P. Gibbs, State University of New York, Syracuse, NY; Thomas P. Hodgman, Maine Department of Inland Fisheries and Wildlife, Bangor, ME; and Peter D. Vickery, The Center for Ecological Conservation, Richmond, ME, “Breeding ecology of sympatric Sharp-tailed Sparrows.”
- Paul Spitzer, Cooperative Oxford Lab, Oxford, MD, “Local impact of Double-crested Cormorant invasion on breeding Ospreys: possible ‘soft parasitism’ on feeding Ospreys in the waters around Gardiners Island, NY.”
- Scott H. Stoleson, USDA Forest Service, Irvine, PA, “Habitat use by Cerulean Warblers in an oak-northern hardwoods transition zone: implications for management.”
- Megan M. Szymanski, Cornell Lab of Ornithology, Ithaca, NY, “High lineage diversity and host sharing of malarial parasites in a local avian assemblage.”
- Jeffrey V. Wells, Cornell Lab of Ornithology, Ithaca, NY, “Demographic and aerographic fragmentation in distributions of North American birds.”
- Kevin Wentworth and Margaret Brittingham, Pennsylvania State University, University Park, PA, “Effects of field characteristics on avian use and productivity in Conservation Reserve Enhancement Program fields and a comparison with hayfields.”
- David W. Winkler, Peter H. Wrege, Paulo E. Llambías, and Valentina Ferretti, Cornell University, Ithaca, NY, “Breeding dispersal in the Tree Swallow (*Tachycineta bicolor*).”
- “Assessment of Black Tern habitat along eastern Lake Ontario.”
- Emily C. Arell and Anna Sommo, Colby College, Waterville, ME, “Characteristics of Downy, Hairy, and Pileated Woodpecker foraging excavations.”
- Colleen E. Bell, Canisius College, Buffalo, NY; Arthur R. Clark, Buffalo Museum of Science, Buffalo, NY; and Sara R. Morris, Canisius College, Buffalo, NY, “Not watching television (towers) can be hazardous to a bird’s health.”
- David Bonter, Cornell Lab of Ornithology, Ithaca, NY, “Study of overwinter survival monitors seasonal mortality in feeder birds.”
- Jennifer Brinks, Patrick A. Thorpe, and Michael P. Lombardo, Grand Valley State University, Allendale, MI, “A direct test of the sexually transmitted microbe hypothesis of avian copulation in Tree Swallows (*Tachycineta bicolor*).”
- Barbara M. Brown, Michael P. Lombardo, and Patrick A. Thorpe, Grand Valley State University, Allendale, MI, “Comparison of digit ratio in male and female House Sparrows.”
- Charles R. Brown and Mary Bomberger Brown, University of Tulsa, Tulsa, OK, “Daily survival probabilities of adult and juvenile Cliff Swallows vary with colony size and ectoparasite load.”
- William P. Brown, University of Delaware, Newark, DE; and Patrick J. Sullivan, Cornell University, Ithaca, NY, “Avian community composition in isolated forest fragments: a new conceptual model.”
- Benjamin M. Clock and Marc S. Dantzker, Cornell Lab of Ornithology, Ithaca, NY, “The Library of Natural Sounds (LNS) becomes a multimedia archive for the study of bird behavior.”
- Kristen M. Covino, Joanna M. Panasiewicz, Sara R. Morris, and H. David Sheets, Canisius College, Buffalo, NY, “In males shape matters: age and sex dimorphism in the feather shape of Red-eyed Vireos.”
- Amy Dabrowski, Cornell Lab of Ornithology, Ithaca, NY; Rachel Fraser, Queen’s University, Kingston, ON, Canada; John Confer, Ithaca College, Ithaca, NY; and Irby Lovette, Cornell Lab of Ornithology, Ithaca, NY, “Geographic variability in mitochondrial introgression among hybridizing populations of Golden-winged and Blue-winged Warblers.”
- Christina E. Donehower and David M. Bird, McGill University, Ste. Anne de Bellevue, QC, Canada; and Stephen W. Kress, National Audubon Society, Ithaca, NY, “Quantifying gull predation at a Maine tern colony.”
- Jerry D. Dudziak, Jennifer M. Urbanski, Sara R. Morris, and H. David Sheets, Canisius College, Buffalo, NY, “Can assemblages of migrating birds be detected using SHEBI analysis?”
- Shannon Ehlers, University of Akron, Akron, OH, “Associations, dispersal, and habitat utilization of juvenile Brown-headed Cowbirds (*Molothrus ater*).”
- Susan Ellis and Margaret Voss, Penn State Erie, The Behrend College, Erie, PA, “Changes in maternal time allocation over incubation.”

POSTERS

- David Adams, New York State Department of Environmental Conservation, Albany, NY; Kevin Kenow and Robert Kratt, U.S. Geological Survey, La Crosse, WI; David Evers, BioDiversity Research Institute, Gorham, ME; Nina Schoch, Adirondack Cooperative Loon Program, Ray Brook, NY; Kate Taylor, Loon Preservation Committee, Moultonborough, NH; and Andrew Major, U.S. Fish and Wildlife Service, Concord, NH, “Migration patterns and wintering range of Common Loons breeding in the northeastern United States: preliminary findings.”
- David Adams, New York State Department of Environmental Conservation, Albany, NY; and Irene Mazzocchi, Bureau of Wildlife, Watertown, NY,

- Miranda C. Ertel, Canisius College, Buffalo, NY; Mary P. Wright, Shoals Marine Laboratory, Cornell University, Ithaca, NY; and Sara R. Morris Canisius College, Buffalo, NY, "The incidence and effects of ticks on migrating birds at a stopover site."
- Andrew Farnsworth, Cornell University, Ithaca, NY, "The prevalence of flight calls in wood-warblers during non-migratory periods."
- Shari Gross and E. Dale Kennedy, Albion College, Albion MI, "Do male House Wrens sing the same songs year to year?"
- Ralph S. Hames and James D. Lowe, Cornell Lab of Ornithology, Ithaca, NY, "Quantifying calcium-rich prey species available to nesting Wood Thrushes in regions with different amounts of acid rain."
- Daniel Hanley, Dana Hawley, and André Dhondt Cornell University, Ithaca, NY, "Are the effects of the eastern House Finch bottleneck evident today? An investigation through the use of allelic and haplotypic diversity."
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by Kathleen G. Beal

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