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MUSEUM
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FOURTH COLLOQUIUM ON CONSERVATION OF MAMMALS IN THE SOUTHEASTERN UNITED STATES

Edited by BRIAN R. CHAPMAN
and JOSHUA LAERM

Occasional Papers of the
North Carolina Museum of Natural Sciences and the
North Carolina Biological Survey
Number 12
Fall, 2000

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Fourth Colloquium on Conservation of Mammals in the Southeastern United States

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Forward

Mammals have been the focus of intensive scientific inquiry and much is known of the life-history attributes of many species. However, recent environmental concerns and new legislation requiring environmental assessments have brought demands for more detailed information on the systematics, population status, and habitat requirements of mammals. It will take the concerted efforts of professional mammalogists from federal and state agencies, academic institutions, and the private sector to establish priorities and meet the mammalian research and conservation needs that society requires.

The "Colloquium" is a loosely organized group of professional scientists from the southeastern United States that has interest in conservation and management of mammals in the region. The group first met at the University of Memphis in 1991 and has met annually since then. The Colloquium exists to provide individuals representing different agencies or institutions to meet, get acquainted, and exchange information and ideas concerning mammalian research and conservation priorities.

The 1994 Colloquium was held at the University of Georgia and was sponsored jointly by the Institute of Ecology and the Daniel B. Warnell School of Forest Resources. The scientific program consisted of 19 contributed papers and two posters. The presentations primarily focused on two areas—the status of selected taxa (especially of protected or little-known species), and aspects of life history. This symposium volume is dedicated to the men and women who initiated and fostered communication and research on mammals in the southeastern United States, to those who have recently added enthusiasm and skill to the crusade, and to those who will contribute to future progress in the conservation of mammal populations and habitats.

Brian R. Chapman

Acknowledgments

This publication represents the results of a colloquium convened in Athens, Georgia, in February 1994, as the Fourth Colloquium on the Conservation of Mammals in the Southeastern United States. This colloquium was made possible by funding and logistical support provided by the Institute of Ecology and the Daniel B. Warnell School of Forest Resources of the University of Georgia.

We thank the 20 anonymous referees who provided excellent reviews of the manuscripts. We express our appreciation to J. L. Boone who provided critical editorial advice on several manuscripts. We also thank the many authors who responded well to advice and criticisms of their work and who waited patiently for their papers to appear in print.

The Editors: Brian R. Chapman,
Joshua Laerm.

FOURTH COLLOQUIUM ON CONSERVATION OF MAMMALS IN THE SOUTHEASTERN UNITED STATES

Edited by
Brian R. Chapman and Joshua Laerm

Contents

COLLOQUIUM ON CONSERVATION OF MAMMALS IN THE SOUTHEASTERN UNITED STATES

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The Colloquium on Conservation of Mammals in the Southeastern United States stemmed from an interest to foster communications and research on mammals by professional biologists working in the Southeast. Earliest discussions of such a conference were held informally by T. L. Best, G. A. Heidt, M. L. Kennedy, P. K. Kennedy, and V. R. McDaniel during the 1980s. The number of professional mammalogists and biologists conducting research and either charged or interested in the conservation of mammalian resources in the southeastern states grew significantly from the 1950s and 1960s to the 1980s. There was a feeling among the early organizers of the Colloquium of a need for better communication among biologists working in this region. A desire of the early organizers was to bring individuals from academic institutions, state and federal agencies, and companies in the private sector together to discuss conservation issues of significance to people in the region, as well as to establish needs and priorities (if possible) for scientific study. A unique feature of this meeting, from the start, was a gathering of professionals from different disciplines with mutual interests in mammals. There was feeling among the early organizers that communication among agencies, as well as among individuals, was a key to success relating to mammalian conservation in the Southeast. The original region of interest was limited to the south-central states (Alabama, Arkansas, Kentucky, Louisiana, Mississippi, Missouri, Tennessee), and, initially, the loosely structured organization was referred to as the Colloquium on Conservation of Mammals in the South-central States. At the 1994 meeting, the geographic region was expanded to include all of the southeastern United States and the organization named appropriately (Colloquium on Conservation of Mammals in the Southeastern United States). A brief history of the Colloquium is presented in the following paragraphs.

On 17 May 1991, the First Colloquium on Conservation of Mammals in the South-central United States was held at The University of Memphis' Edward J. Meeman Biological Station in Shelby Co., Tennessee. The meeting focused on conservation biology and was sponsored by the Edward J. Meeman Biological Station, College of Arts and Sciences, and Office of Public Service at The University of Memphis. The meeting was hosted by M. L. Kennedy, and, for this first meeting, papers and participants (39 attended) were invited. Following an official welcome by Associate Dean H. D. Black, J. K. Jones, Jr., spoke during the Plenary Session. His talk was entitled "Concerns for Mammalian Biodiversity and Bioconservation in the South-central States." G. A. Heidt, V. R. McDaniel, and J. P. Nelson, Jr., served as chairpersons for three paper sessions. Paper sessions were followed by a panel discussion entitled "Priorities in Mammalian Bioconservation in the South-central States." Panel members included V. R. McDaniel (Chair), J. K. Jones, Jr., T. L. Best, and G. A. Heidt. The meeting concluded with a wrap up and discussion of future plans. Participants voiced a "successful meeting" and voted to make the meeting an annual event. Informal discussions tended to indicate that the best time for the annual meeting would be in February. It was decided that the second meeting should be in northern Alabama (to be hosted by T. L. Best, Auburn University).

The Second Colloquium on Conservation of Mammals in the South-central United States was held at Guntersville State Park in northern Alabama on 20-21 February 1992. The meeting was sponsored by the Department of Zoology and Wildlife Science at Auburn University. A pre-meeting social during the evening of the 20th was well attended. Forty-eight participants attended the meeting on the 21st. J. F. Pritchett (Head, Department of Zoology and Wildlife Science) extended the official welcome. The Plenary Session was a paper entitled "Problems in the Conservation of Small Mammals: Beach Mice as an Example" presented by N. R. Holler. A panel discussion on "Problems and Prospects for Conservation of Mammals in the South-central United States" followed. Members of the panel included M. L. Kennedy (Chair), R. K. Chesser, N. R. Holler, R. Jordan, V. R. McDaniel, and M. C. Wooten. The remainder of the formal program included one poster and 12 paper presentations. This was another very successful meeting. The interaction of individuals from different institutions and agencies was very high. It was decided that the third meeting would be in Arkansas (to be hosted by G. A. Heidt, University of Arkansas at Little Rock, and V. R. McDaniel, Arkansas State University). A very successful field trip (led by T. L. Best) to Blowing Wind Cave followed the meeting.

On 25-26 February 1993, the Third Colloquium on Conservation of Mammals in the South-central United States was held at the Ozark Folk Center State Park, Mountain View, Arkansas. The meeting was co-sponsored by the Department of Biology at the University of Arkansas Little Rock and Department of Biological Sciences at Arkansas State University. Despite snowy weather, the pre-meeting social on the evening of the 25th was well patronized. Forty-three participants attended the meeting on the 26th. Technical sessions were chaired by T. L. Best, J. Laerm, C. R. Tumlison, and J. P. Nelson. Twenty papers were presented. At the conclusion of the paper sessions, a roundtable discussion was held among all participants regarding conservation issues of concern. Future direction and plans for the Colloquium also were discussed. A field trip to Blanchard Springs Caverns was cancelled due to bad weather. Participants believed that the meeting had been very successful and decided that the fourth meeting would be held in Georgia (to be hosted by J. Laerm and B. Chapman).

The Fourth Colloquium on Conservation of Mammals in the Southeastern United States was held on the campus of the University of Georgia in Athens on 25-26 February 1994. Hosts arranged an outstanding reception for participants on the evening of the 25th at the Museum of Natural History. Food was bountiful, beverages copious, atmosphere biological, and interaction among participants excellent. On the morning of the 26th, J. Laerm extended an official welcome to the group. Three technical sessions followed (chaired by J. Laerm, B. Chapman, and M. L. Kennedy). Nineteen oral and two poster presentations were presented. A roundtable discussion included remarks relating to a number of conservation issues. A decision was made to publish a journal issue that would contain selected papers presented at the Fourth Colloquium, as well as papers solicited from other researchers in the southeastern United States. About 80 participants attended the meeting. M. J. Harvey invited the group to meet in Tennessee in 1995.

On 24-25 February 1995, the Fifth Colloquium on Conservation of Mammals in the Southeastern United States was held at the Executive Inn in Cookeville, Tennessee. The meeting was sponsored by the Department of Biology at Tennessee Tech University. Following the informal reception on the 24th, M. J. Harvey extended an official welcome on the morning of the 25th. Three paper sessions (chaired by B. Cushing, J. P. Nelson, and M. J. Lacki, respectively) followed. Seventeen papers and two posters were presented. The first paper entitled “Conservation Mammalogy in and Around Tennessee” by M. J. Harvey got the day off to an excellent start. The day ended with a discussion session relating to conservation of mammals in the southeastern United States; business relating to the journal issue and the next annual meeting were discussed. This was another highly successful meeting. M. J. Lacki invited the group to hold the Sixth Colloquium in Kentucky.

Since the 1995 meeting in Cookeville, the Colloquium on Conservation of Mammals in the Southeastern United States has held four additional meetings. Locations and hosts were as follows: 1996 (sixth meeting)—Kentucky Leadership Center, Somerset, Kentucky (M. J. Lacki, University of Kentucky); 1997 (seventh meeting)—YMCA Blue Ridge Assembly, Black Mountain, North Carolina (M. K. Clark, North Carolina State Museum of Natural Science); 1998 (eighth meeting)—Arlington Hotel, Hot Springs, Arkansas (D. A. Saugey, Ouachita National Forest, United States Forest Service); 1999 (ninth meeting)—Holiday Inn, Wytheville, Virginia (R. Reynolds, Virginia Department of Game and Inland Fisheries). The ninth meeting was sponsored by Virginia Department of Game and Inland Fisheries, Ferrum College, Westvaco, George Washington and Jefferson national forests, and Virginia Department of Conservation and Recreation, Division of Natural Heritage.

Beginning in 1996, the Colloquium has met jointly with the Southeastern Bat Diversity Network. Format of the meeting has included a day focused on topics relating to bats and another on conservation of mammals in the region. This joint meeting seemed natural because many individuals associated with the Colloquium also were interested in bats occurring in the southeastern United States. In 1999, an ad hoc Allegheny Woodrat Recovery Team met concurrently with the Colloquium and the Southeastern Bat Diversity Network.

The Colloquium and the field of conservation suffered a great loss in 1997 with the death of Dr. Joshua Laerm (University of Georgia). The 1998 meeting in Hot Springs was special in that it was dedicated to the memory of Dr. Laerm. The meeting was outstanding in all regards.

An assessment of the Colloquium after 9 years would seem to indicate that the goals of the early organizers are being met. Each meeting has been somewhat larger than the previous one in attendance, and communications among individuals working in the Southeast have been improved, especially among academic institutions and state and federal agencies. An annual newsletter prepared by J. P. Nelson at Bethel College contributed in the most positive manner toward promoting exchange of information during the first 5 years of the Colloquium. Most encouraging has been the discussions among participants of the Colloquium relating to mammalian conservation on a regional scale in addition to state levels. Individuals that have participated in the meetings and shared information with others in the region are to be commended. Because of the many concerns relating to conservation of mammals in the region, meetings like the Colloquium will play a major role in identifying problems and fostering solutions. Overall, the future of the Colloquium appears to be very bright. Planning for the 10th annual meeting (to be held in Alabama and hosted by T. L. Best, Auburn University) is in progress, and it promises to be another outstanding meeting. All individuals with an interest in mammalian conservation in the southeastern United States are invited to attend the annual meeting and participate in all parts of the program.

CONSERVATION STATUS OF TERRESTRIAL MAMMALS OF THE SOUTHEASTERN UNITED STATES

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We reviewed the conservation status of terrestrial mammals of the southeastern United States based on taxa listed as endangered, threatened, rate, or of special concern under federal, state, and Natural Heritage Program guidelines. Of the 101 species of terrestrial mammals that occur in the southeastern United States, 78 (77.2%) are viewed as sensitive from a conservation perspective. Of the 276 currently recognized taxa (monotypic species plus subspecies of polytypic species), 137 (49.6%) known to occur in the region are viewed as sensitive. Sixteen species (15.6% of the regional species richness), including 23 taxa (8.3% of the total taxonomic richness), currently are listed as threatened or endangered under federal guidelines. Two taxa are candidates for listing under federal guidelines. At the state level, 62 species (61.4%) comprising 80 taxa (or 32.2%) officially are listed under respective state guidelines as endangered, threatened, rare, or of special concern. The Heritage Inventory Program lists of the respective states include an additional 16 species (including 42 taxa) beyond those listed under various federal and official state guidelines. Of the 21 families of mammals in the region, all but five have one or more sensitive taxa. For all families, the mean number of sensitive taxa relative to total species richness is 68.7%. Current knowledge of taxonomy, distribution, and life-history attributes of many sensitive taxa in the southeastern United States is too poor to adequately assess their conservation status.

Pursuant to the Endangered Species Act of 1973, several agencies of the United States Government have been authorized to compile lists of species, subspecies, or distinct population segments of species that are either endangered or threatened, as defined by law, following appropriate review (Bean, 1993; Wilcove et al., 1993). In addition, the respective states have initiated their own lists and protective regulations of taxa regarded as endangered, threatened, rare, or of special concern. Furthermore, within most state governments, Heritage Inventory programs have developed another set of species categories and lists to meet their own conservation imperatives. The emphasis on, and concern for, listed species and subspecies has become the focus around which many conservation efforts have revolved (Lazell, 1993).

A primary focus of this colloquium, and others in the series, was to provide regionally focused biologists a perspective from which research and education regarding conservation concerns of mammals in the region can be initiated. To identify various taxa of terrestrial mammals in the southeastern United States sensitive from a conservation perspective, we undertook a review of the regional taxa and their status with regard to federal, state, and Heritage Inventory lists. A comprehensive review of the status of each sensitive mammalian taxon in the region clearly is beyond the scope of this paper. Our intent is to focus attention of professional biologists and representatives of various state and federal agencies on those taxa that are viewed as sensitive in the region. We hope that identification of these taxa on a regional basis will foster greater understanding of problems associated with listed species and enhance opportunities for support of more thorough studies.

MATERIALS AND METHODS

The southeastern United States was defined as the Southern Region of the United States Department of Agriculture Forest Service, and includes Virginia, North Carolina, South Carolina, Georgia, Florida, Alabama, Mississippi, Louisiana, Tennessee, Kentucky, Arkansas, and the eastern portions of Texas and Oklahoma. We reviewed standard references (Hall, 1981; Jones et al., 1992; Wilson and Reeder, 1993) and current literature to produce a list of mammalian species that occur in the region. We included all extant native species and introduced species with established regional populations *(Rattus norvegicus, R. rattus, Mus musculus, Myocastor coypus, Sus scrofa).* We did not include taxa known to be extirpated (e.g., *Canis lupus, Bos bison, Cervus elaphus).*

We determined total taxonomic richness through direct counts of monotypic species, plus currently recognized subspecies of polytypic species. We were aware of controversy regarding taxonomy of numerous populations. To resolve these controversies we used standard references (Hall, 1981; Jones et al., 1992; Wilson and Reeder, 1993) and current literature. Departures from these authorities are discussed in Appendix I.

We compiled a faunal list of those terrestrial mammalian species and subspecies that were considered to be sensitive from a conservation perspective. These included: 1) taxa listed as endangered, threatened, or candidates for listing under United States Fish and Wildlife Service guidelines prior to suspension of formal candidate-species designation (United States Fish and Wildlife Service, 1993, 1996); 2) taxa listed as endangered, threatened, rare, or of special concern under respective official state guidelines; 3) taxa monitored or tracked under various Heritage Inventory programs in the respective states. Official state-listed taxa and those on Heritage Inventory lists were obtained from the respective states.

We did not intend to provide a comprehensive evaluation of the status of each sensitive taxon identified in our analysis. New federal listings and rulings are issued frequently. State lists are updated and changed on a yearly basis. Heritage Inventory lists are subject to continuous change. However, we believe that errors of inclusion or exclusion would not significantly alter our results qualitatively or quantitatively.

Because respective state and Heritage Inventory lists do not always specify subspecific affinities of species considered sensitive, we have attempted to refer populations in that state to particular subspecies, where possible, based on published range maps. We do not believe that this exaggerates the numbers of sensitive taxa. Rather, this permits a clearer view of the problem with respect to total regional taxonomic richness.

RESULTS

In the southeastern United States, there are 101 species of terrestrial mammals, including 276 individual taxa. These are listed in Table 1. We included only those subspecies listed as sensitive and indicate their status with respect to federal, state, and Heritage Inventory lists. Of the 101 species that occur regionally, 78 (77.2%) occur on one or another of the lists of sensitive species. Furthermore, of the 276 individual taxa, 128 (46.4%) are considered sensitive.

Sixteen species, including 23 taxa, currently are listed as threatened or endangered under federal guidelines (United States Fish and Wildlife Service, 1993). These represent 15.6% of the species richness and 8.3% of the total mammalian taxonomic richness in the region, respectively. Three taxa are listed as threatened and the remainder are listed as endangered. In addition, two taxa are current candidates for listing (United States Fish and Wildlife Service, 1996). All federally listed endangered or threatened taxa also are listed in the respective states in which populations occur. Of the 23 federally listed taxa, three *(Myotis grisescens, M. sodalis, and Canis rufus)* are listed throughout the range of the species. The remaining 20 listed taxa are subspecies or populations of more widely ranging species, and only designated subspecies or populations are listed.

Sixty-two species (61.4% of the species richness), including 87 taxa (or 32.3% of the total richness), are listed under respective state guidelines as endangered, threatened, rare, of special concern, or deemed in need of management. The Heritage Inventory programs of the respective states list an additional 16 species, including 42 taxa beyond those listed under various federal and official state guidelines.

In the southeastern United States, 21 families of mammals occur, and all but five (Didelphidae, Dasypodidae, Castoridae, Myocastoridae, Suidae) have one or more sensitive taxa (Table 2). In the remaining 16 families, percentage of sensitive species relative to total species richness ranges from a low of 50% (Canidae) to a high of 100% (Talpidae, Molossidae, Leporidae, Geomyidae, Heteromyidae, Dipodidae, Canidae, Procyonidae, Cervidae). In 10 families (essentially one-half of the total family richness in the region), every species has one or more subspecies listed as sensitive. For all families, mean number of sensitive species relative to total species richness is 68.7%.

Percentage of sensitive taxa per family relative to total taxonomic richness ranges from a low of 21% in the Procyonidae to a high of 100% in the Molossidae, Dipodidae, and Ursidae. We note that those families with 100% of taxa listed as sensitive are among the least speciose in the region. However, the proportion of sensitive

Table 1.—*Mammalian taxa of the southeastern United States and their conservation status under federal (USA) and respective state guidelines: C, candidate for federal listing; D, deemed in need of management; E, endangered; H, monitored by Heritage Inventory Program; P, protected; R, rare; SC, special concern, T, threatened. All regional species are listed, but only those subspecies identified as sensitive as included.*

Taxon	USA	AL	AR	FL	GA	KY	LA	MS	NC	OK	SC	TN	TX	VA
Order Didelphimorphia														
FamilyDidelphidae														
Didelphis virginiana														
Order Insectivora														
Family Soricidae														
Sorex cinereus					H	SC					SC	D		
S. c. cinereus						SC								
S. c. lesueurii														
Sorex longirostris														
S. l. eionis				SC										
S. l. fisheri	T								T					T
S. l. longirostris			H	H			H	H				D		
Sorex palustris														
S. p. punctulatus									SC			D		E
Sorex fumeus														
S. f. fumeus											SC	D		
Sorex dispar														
S. d. blitchi						E			SC			D		
Sorex hoyi														
S. h. winnemana					H				SC		SC	H		
Blarina brevicauda														
Blarina carolinensis														
B. c. shermani				SC										
Blarina hylophaga														
Cryptotis parva														
Notiosorex crawfordi														
N. c. crawfordi			H							SC				
Family Talpidae														
Parascalops breweri											SC	D		
Scalopus aquaticus														
Condylura cristata														
C. c. parva					H				SC		SC	D		
Order Chiroptera														
Family Vespertilionidae														
Myotis leibii			H		H	E			SC	SC	T	D	H	H
Myotis lucifugus														
M. l. lucifugus	H							H		H	SC			
Myotis sodalis	E	E	E	E	E	E		E	E	E	E	E		E
Myotis austroriparius		P	H	H	H	E			SC	SC	T	H	H	
Myotis grisescens	E	E	E	E	E	E		E	E	E		E		E

Table 1.—*continued*

Taxon	USA	AL	AR	FL	GA	KY	LA	MS	NC	OK	SC	TN	TX	VA
Family Vespertilionidae *(continued)*														
Myotis septentrionalis		H	H	H				H	SC	H	SC			
Lasionycteris noctivagans							H	H		H				
Pipistrellus subflavus														
Eptesicus fuscus														
E. f. fuscus				H			H							
E. f. osceola				H										
Lasiurus intermedius														
L. i. floridana		H			H			H			SC			H
Lasiurus borealis														
Lasiurus seminolus		H								SC				H
Lasiurus cinereus				H				H			SC			
Nycticeius humeralis														
N. h. humeralis						T								
Corynorhinus rafinesquii														
C. r. macrotis		P	H	H	R			H	SC	SC	E		T	E
C. r. rafinesquii		P	H		R	T		H	SC		E			E
Corynorhinus townsendii														
C. t. ingens	E		E							E				
C. t. virginianus	E					E			E			H		E
Family Molossidae														
Tadarida brasiliensis														
T. b. cynocephala		P	H						SC	SC				
Eumops glaucinus														
E. g. floridanus				E										
Order Xenarthra														
Family Dasypodidae														
Dasypus novenscinctus												H		
Order Lagomorpha														
Family Leporidae														
Sylvilagus palustris														
S. p. hefneri	E			E										
S. p. palustris		H												SC
Sylvilagus floridanus														
S. f. hitchensi													H	
Sylvilagus obscurus		H			R				H		H	H		
Sylvilagus aquaticus														
S. a. aquaticus									H	H	SC	H		
Lepus americanus														
L. a. virginianus														E
Lepus californicus														
L. c. melanotis			H											

Table 1.—*continued*

Taxon	USA	AL	AR	FL	GA	KY	LA	MS	NC	OK	SC	TN	TX	VA
Order Rodentia														
Family Sciuridae														
Tamias striatus														
T. s. striatus				SC										
Marmota monax														
M. m. monax										SC				
Sciurus carolinensis														
Sciurus niger														
S. n. avicenia				T										
S. n. cinereus	E													E
S. n. niger									H		SC			H
S. n. shermani				SC	H									
Tamiasciurus hudsonicus														
T. h. abieticola					H						SC			
Glaucomys volans														
Glaucomys sabrinus														
G. s. coloratus	E								E			E		
G. s. fuscus	E													E
Family Geomyidae														
Geomys breviceps														
Geomys pinetis														
G. p. pinetis		P												
G. p. fontanelus					H									
Family Heteromyidae														
Chaetodipus hispidus														
C. h. hispidus							H							
Family Castoridae														
Castor canadensis														
Family Muridae														
Oryzomys palustris														
O. p. natator (=argentatus)		E		E										
O. p. natator (=planirostris)				H										
O. p. natator (=sanibel)				SC										
O. p. palustris											H			
Reithrodontomys montanus														
R. m. griseus			H											
Reithrodontomys humulis														
R. h. humulis			H				H							
R. h. merriami			H				H			SC				
Reithrodontomys megalotis														
Reithrodontomys fulvescens														

Table 1.—*continued*

Taxon	USA	AL	AR	FL	GA	KY	LA	MS	NC	OK	SC	TN	TX	VA
Family Muridae *(continued)*														
Peromyscus polionotus														
P. p. allophrys	E			E										
P. p. ammobates	E	E												
P. p. colemani								H	H					
P. p. decoloratus				H										
P. p. leucocephalus				H										
P. p. niveiventris	T			T										
P. p. peninsularis	C			E										
P. p. phasma	E			E										
P. p. trissyllepsis	E	E		E										
Peromyscus maniculatus														
Peromyscus leucopus														
P. l. easti									H					
Peromyscus gossypinus														
P. g. allapaticola	E			E										
P. g. anastasae				H	H									
P. g. megacephalus						T								
P. g. restrictus				H										
Peromyscus attwateri														
Podomys floridanus				SC										
Ochrotomys nuttalli														
O. n. flammeus										SC				
Baiomys taylori														
Sigmodon hispidus														
S. h. exsputus					H									
S. h. insulicola				H										
Neotoma floridana														
N. f. floridana									T		SC			
N. f. haematoreia					H				SC		H	D		
N. f. illinoiensis					H							D		
N. f. smalli	E			E										
Neotoma magister		H				H			SC			D		
Rattus norvegicus														
Rattus rattus														
Mus musculus														
Clethrionomys gapperi														
C. g. carolinensis					H						SC			
C. g. maurus						SC								
Microtus pennsylvanicus														
M. p. dukecampbelli	E			E										
M. p. pennsylvanicus											SC			

Table 1.—*continued*

Taxon	USA	AL	AR	FL	GA	KY	LA	MS	NC	OK	SC	TN	TX	VA
Family Muridae *(continued)*														
Microtus chrotorrhinus									SC					
M. c. carolinensis						SC			D			E		
Microtus ochrogaster														
M. o. ochrogaster		H												
Microtus pinetorum														
Neofiber alleni														
N. a. alleni				H										
N. a. apalachicolae				H										
N. a. exoristus					T									
N. a. nigrescens				H										
N. a. struix				H										
Ondatra zibethicus														
Synaptomys cooperi														
S. c. stonei												D		
Family Dipododae														
Zapus hudsonius														
Z. h. americanus		P									SC	D		
Z. h. intermedius								H				D		
Z. h. pallidus										SC				
Napaeozapus insignis														
N. i. roanensis											SC	D		
Family Myocastoridae														
Myocastor coypus														
Order Carnivora														
Family Canidae														
Canis latrans														
Canis rufus	E			H			E		E	E		E	H	
Vulpes vulpes														
V. v. fulva			H											
Urocyon cinereoargenteus														
Family Ursidae														
Ursus americanus														
U. a. americanus						SC		E	H	H	SC	H	E	
U. a. floridanus	C	H		T										
U. a. luteolus	T						T	E					E	
Family Procyonidae														
Bassariscus astutus														
B. a. flavus			H				H			SC				
Procyon lotor														
P. l. auspicatus				H										

Table 1.—*continued*

Taxon	USA	AL	AR	FL	GA	KY	LA	MS	NC	OK	SC	TN	TX	VA
Family Mustelidae														
Martes pennanti														
M. p. pennanti														H
Mustela nivalis														
M. n. allegheniensis						SC			H		SC	H		H
Mustela frenata														
M. f. arthuri							H							
M. f. olivacea				H										
M. f. peninsulae				H										
M. f. primulina			H				H			SC				
Mustela vison														
M. v. mink (=evergladensis)				T										
M. v. halilimnetes				H										
M. v. lutensis				H										
M. v. mink				H										
Taxidea taxus														
T. t. berlandieri			H											
Spilogale putorius														
S. p. interrupta							H			H			H	
S. p, putorius		H				SC	H				SC	H	H	
Mephitis mephitis														
Conepatus mesoleucus														
C. m. telmalestes													H	
Lontra canadensis														
L. c. lataxina			H							SC		T		
Family Felidae														
Puma concolor														
P. c. coryi	E	E	E	E	H		E	E			SC	E		
P. c. couguar	E				H				H		E			E
P. c. stanleyana									SC					
Lynx rufus														
L. r. floridanus				H										
Order Artiodactyla														
Family Suidae														
Sus scrofa														
Family Cervidae														
Odocoileus virginianus														
O. v. clavium	E			E										
O. v. hiltonensis											H			
O. v. nigribarbis					H									
O. v. taurinsulae											H			
O. v. venatoria											H			

taxa in the more speciose families also is high. For example, 11 (50%) of the 22 recognized soricid taxa are considered sensitive. There are 21 taxa included in the 16 regional species of vespertilionid bats, of which 17 (81%) are listed as sensitive. Similarly, in the most speciose regional family, Muridae, which includes 94 taxa in 27 species, 40 (42.1%) taxa are listed as sensitive. High percentages of sensitive taxa also are seen in the mustelids where 15 (71.4%) of the 21 taxa are listed.

Mean number of federally listed threatened and

Table 2.—*Taxonomic diversity and numbers of problematic taxa by family. Number of taxa includes total number of monotypic species plus subspecies of polytypic species.*

	Diversity		Problematic taxa			
Taxon	Number of species	Number of taxa	Number of species	Percentage	Number of taxa	Percentage
DIDELPHIMORPHIA						
Didelphidae	1	2	0	0	0	0
INSECTIVORA						
Soricidae	11	22	8	72.7	11	50
Talpidae	3	13	2	66.7	2	15.4
CHIROPTERA						
Vespertilionidae	16	21	14	87.5	17	81
Molossidae	2	2	2	100	2	100
XENARTHRA						
Dasypodidae	1	1	1	100	1	100
LAGOMORPHA						
Leporidae	6	16	6	100	7	43.7
RODENTIA						
Sciuridae	7	26	5	71.4	9	34.6
Geomyidae	2	5	2	100	2	40
Heteromyidae	1	2	1	100	1	50
Castoridae	1	5	0	0	0	0
Muridae	27	95	17	63	40	42.1
Dipodidae	2	4	2	100	4	100
Myocastoridae	1	1	0	0	0	0
CARNIVORA						
Canidae	4	6	2	50	2	33.3
Ursidae	1	3	1	100	3	100
Procyonidae	2	14	2	100	3	21.4
Mustelidae	9	21	8	88.9	15	71.4
Felidae	2	6	2	100	4	66.7
ARTIODACTYLA						
Suidae	1	1	0	0	0	0
Cervidae	1	10	1	100	5	50
Total		101	276	75		128

Table 3.—*Federal, state, and Heritage Inventory Program listings of sensitive terrestrial mammalian taxa in the southeastern United States.*

State	Federal listed	Federal proposed	State listed[a]	Heritage inventory listed[b]	Total listed[c]
Alabama	5	1	10	10	20
Arkansas	4		4	15	19
Florida	14	2	24	20	44
Georgia	5	1	7	17	24
Kentucky	3		14	1	15
Louisiana	3		3	8	11
Mississippi	4		5	9	14
North Carolina	7		20	7	27
Oklahoma[d]	5		18	6	24
South Carolina	2		5	26	31
Tennessee	6		22	9	31
Texas[d]	2		2	3	5
Virginia	7		12	7	19

[a] State-listed taxa include federally listed taxa.
[b] Heritage Inventory listings beyond federal and state listings.
[c] Total taxa listed by respective states.
[d] Eastern portions of these states only.

endangered taxa per state is 5.3, and mean number of state-listed taxa is 11.2 (Table 3). Mean number of taxa listed by Heritage Inventory programs per state is 10.6. Mean number of sensitive taxa per state is 21.8.

DISCUSSION

The southeastern region of the United States includes only a small proportion (ca. 8%) of the total North American mammalian fauna (ca. 3,600 total named taxa—Hall, 1981). Although we have not addressed sensitive mammalian taxa at the faunal scale of North America, we believe that our regional examination probably reflects the scope of conservation concerns for other portions of North America.

Our survey indicates a significant proportion of terrestrial mammals in the southeastern United States is viewed as sensitive from one perspective or another. Although 77% of all species and 49% of all named taxa in the region may be considered sensitive, there is no compelling evidence that all or even most of these taxa are imperiled. Except for the 23 taxa listed under federal guidelines as endangered or threatened, and a few other well-studied taxa, there is only limited evidence regarding the population status or actual threats to survival of many of the remaining taxa. At present, too little information regarding aspects of taxonomy, distribution, and life-history attributes of many of these taxa is available to adequately determine their status (e.g., Caire et al., 1989; Choate et al., 1994; Handley, 1991; Humphrey, 1992; Kennedy and Harvey, 1981; Laerm, 1981; Lee et al. 1982; Schmidly, 1983; Sealander and Heidt, 1990; Webster et al., 1985). Based upon our review, we suggest that the high proportion of listed taxa, particularly on state and Heritage Inventory lists, is more a reflection of lack of knowledge and uncertainty of the true status of these taxa, as opposed to a clear indication that most (or even some) of these are under any threats to their survival.

Lack of knowledge of basic aspects of taxonomy, distribution, and life history of many, if not most, of these taxa is in part a reflection of the agenda of the conservation community, agencies with conservation mandates, and individual scientists. Traditionally, most attention has been focused on the more charismatic and higher-visibility federally endangered and threatened taxa. Recently, conservation concerns have shifted from single species to habitats and ecosystems. While most biologists would recognize the basic importance and relevance of systematic, distributional, and life-history studies to conservation biology, few biologists are willing to undertake such studies, and fewer agencies are willing to fund such studies. We recognize that few biologists with training in modern morphometric and molecular techniques are available to focus on local and regional taxonomic problems. Those biologists with the training, expertise, and resources (generally limited to major universities) tend to focus on broader conceptual systematic issues. Descriptive distributional and life-history studies often are considered a bane to the career of professional academic or museum researchers at major institutions. Publications resulting from these types of studies usually are relegated to regional or state journals. Funding opportunities are almost nonexistent for regional systematic, distributional, and life-history studies, except for small grants through state nongame programs. Such grants seldom are adequate to permit comprehensive regional surveys, much less the in-depth and long-term, life-history studies necessary to assess the status of some taxa.

Whatever the motivations and agendas of state and federal agencies, conservation groups, individual scientists, and citizens may be, we believe that recognition of the scope of conservation concerns regarding mammals and the recognition of sensitive taxa is the first step in resolution of these concerns. Furthermore, taxonomic, distributional, and life history are absolutely fundamental, hence critical, to a clear understanding and resolution of conservation problems.

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Appendix I

We recognize there may be some controversy regarding recognition of certain taxa at the species level since (and including) Hall (1981); however, we have deferred to Jones et al. (1982, 1986, 1992), as well as Wilson and Reeder (1993) and references therein. Significant departures from these sources include the following.

Sorex cinereus fontinalis—Following Handley (1982), we do not include this subspecies as occurring in Virginia.

Tamias striatus pipilans—As indicated by Jones and Sutkus (1979), *T. s. pipilans* is not distinct from *T. s. striatus.*

Geomys breviceps—Has been regarded as distinct from *G. bursarius* based upon cytological and protein allozyme differences. Two subspecies are recognized regionally; the geographically restricted *G. b. breviceps* and wide-ranging *G. b. sagittalis* (Bohlin and Zimmerman, 1982; Honeycutt and Schmidly, 1979).

Geomys cumberlandius—Contrary to Wilson and Reeder (1993) and Setzer (1989a) who recognize two subspecies in the *Oryzomys palustris* complex; *natator*

(*=argentatus, coloraltus, planirostris,* and *sanibeli)* and *palustris (=palustris* and *texensis).* However, we number as separate those populations previously referred to as argentatus, planirostris, and sanibeli in our list of sensitive taxa following the Florida Game and Fresh Water Fish Commission (1994) and Florida Natural Areas Inventory lists.

Neotoma magister—We follow Hayes and Richmond (1993) in recognition of *N. magister* as a distinct species.

Neofiber alleni—We are sympathetic to Burt's (1954) criticism on the over splitting of *N. alleni,* but we retain the currently recognized subspecies listed by Hall (1981).

Mustela vison complex—We follow Humphrey and Setzer (1989b) who described *M. v. halilimnetes.* We also follow their synonymy of *M. v. evergladensis* and *M. v. mink.* However, as in the case of *aoryzomys,* we list as separate the former *"evergladensis"* population because it is still listed as threatened by the Florida Game and Fresh Water Fish Commission (1994).

Canis rufus—Largely in response to the recent controversy regarding the species-level distinction of *Canis rufus* (e.g., Avise, 1994; Nowak, 1992; Phillips and Henry, 1992; Wayne, 1992), we have not recognized separate subspecies.

ANALYSIS OF DISTRIBUTION AND HABITAT ASSOCIATIONS OF *SOREX HOYI WINNEMANA* IN THE SOUTHERN APPALACHIANS

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We undertook pitfall surveys for the pygmy shrew, *Sorex hoyi winnemana,* throughout the southern Appalachian highlands. Pygmy shrews were captured at 102 (53%) of 190 sites surveyed. While nowhere abundant, the species is widely distributed in a diversity of vegetational and successional states of forest communities. Relative abundance was not well correlated with elevation, aspect, or slope. No difference in relative abundance was detected among vegetational community types; however, significant differences in relative abundance were detected between physiographic regions, with sites in the Ridge and Valley province showing highest relative abundance. Correlation analysis of number of specimens captured and rate of capture revealed poor correlation with microhabitat and macrohabitat features in habitats examined. Review of known distributional records and habitat associations throughout the southeastern United States indicate the pygmy shrew to be much more widely distributed in a diversity of habitat types than previously known. New distributional records for Pennsylvania and Maryland suggest the taxonomic distinction of *S. h. winnemana* to be suspect.

Until recently, the pygmy shrew, *Sorex hoyi winnemana,* was regarded as one of the rarest mammals in the eastern United States. At the time of Diersing's (1980) revision and Handley et al. (1980), there were only 17 records known in the region extending from southern Illinois eastward to Maryland and southward through the Appalachian highlands to Georgia. However, over the past 15 years, pitfall trapping has provided considerable information on distribution, abundance, and habitat associations of the pygmy shrew, particularly in the southeastern United States. At present, the pygmy shrew is monitored by Heritage Inventory programs in Georgia, North Carolina, South Carolina, and Tennessee, protected as a species of special concern in North Carolina, and considered a sensitive species by the United States Department of Agriculture Forest Service.

Because of concerns regarding the conservation status of the pygmy shrew, and other soricids, we initiated extensive surveys throughout the southern Appalachian highlands to more clearly document distributions and habitat associations of these species. We report on results of those surveys as they relate to the pygmy shrew and review distributional records for the species throughout its range.

MATERIALS AND METHODS

During July 1993-August 1995, we established a total of 190 pitfall-trapline transects throughout the southern Appalachian highlands of Georgia, North Carolina, and South Carolina. At each site, 20 pitfalls (0.95-l plastic containers) were placed at or below ground level adjacent to forest-floor debris, including fallen logs, stumps, and rocks at ca. 10-m intervals. Pitfalls were filled with 0.15 l of preservative. Skulls of all specimens were examined and accessioned into collections of the University of Georgia Museum of Natural History.

Elevation, aspect, slope, and forest cover type were recorded for each site. Elevation was recorded to the nearest 20-foot contour from United States Geological Survey topographic maps and converted to meters. Elevation ranged from 200 to 1,525 m above sea level. Aspect was assigned the following values: southwest-facing sites, 0 (the most xeric aspect); west and south, 0.5; northwest and southeast, 1.0; north and east, 1.5; northeast, 2.0. Slope was estimated visually and assigned the following values: flat, 1; sloping, 2; steep slope, 3; cliff face, nearly vertical, 4 (Ford et al., 1994). We examined correlation between mean captures/100 trap nights at each site and elevation, slope, and aspect value using Pearson product-moment correlation.

We characterized forest cover into general community types. 1) Northern hardwoods, typical of higher elevations (usually >1,200 m) and north-facing slopes, and dominated by yellow birch *(Betulla alleghaniensis),* black birch *(B. lenta),* yellow buckeye *(Aesculus octandra),* northern red oak *(Quercus rubrum),* beech *(Fagus grandifolia),* striped maple *(Acer pennsylvanicum),* and mountain maple *(A. spicatum).* Rosebay rhododendron *(Rhododendron maxima)* is a common midstory associate on mesic sites and flame azalea *(R. calendulaceum)* on drier sites. 2) Cove hardwoods occur from ca. 600 to almost 1,200 m and are characteristic of moist, north-facing slopes and sheltered ravines. These communities are dominated by yellow poplar *(Liriodendron tulipifera),* yellow buckeye, basswood *(Tilia hetyerophyla),* black cherry *(Prunus serotina)* northern red oak, and white oak *(Quercus alba).* Cove-hardwoods are noted for their rich herbaceous understory, particularly early spring ephemerals. A well-developed ericaceous midstory rarely is present. 3) Upland-hardwood communities occur at all elevations. They are dominated by northern red oak, white oak, black oak *(Q. velutina),* hickories *(Carya),* blackgum *(Nyssa sylvatica),* and often a midstory shrub layer dominated by American chestnut *(Castaenea dentata),* flame azalea, and rosebay rhododendron on the more mesic sites, or mountain laurel *(Kalmia latifolia)* on the more xeric sites. 4) Mixed pine-hardwoods are present on xeric ridgetops and south-facing slopes, particularly at low-to-mid elevations. These stands are dominated by chestnut oak *(Q. prinus),* scarlet oak *(Q. coccinea),* sourwood *(Oxydendrum arboreum),* and blackgum, with white pine *(Pinus strobus),* pitch pine *(P. rigida),* Virginia pine *(P. virginiana),* and sometimes Table Mountain pine *(P. pungens)* occurring, depending upon moisture, aspect, and elevation. Thick growths of mountain laurel, greenbrier *(Smilax),* and blueberries *(Vaccinium)* usually are present. 5) White pine-eastern hemlock *(Tsuga canadensis)* communities most frequently are associated with riparian zones including a dense rosebay rhododendron-shrub layer. 6) Yellow pine communities dominated by shortleaf pine *(P. echinata)* and southern red oak *(Q. falcata)* are common in upland habitats at lower elevations. 7) Riverine-corridor sites include shrubland islands and sandbars typically associated with sycamore *(Platanus occidentalis)* and sweetgum *(Liquidambar styraciflua).* We compared mean number of captures/100 trap nights in the seven habitat types using a one-way analysis of variance. When significant effects were detected ($P < 0.05$), we performed multiple pairwise comparisons using Tukey's test. We also calculated spatial niche breadth of *S. hoyi* following Levins (1968) and Sheftel (1994).

Given the complexity of environmental variables (e.g., geomorphology, elevation, vegetational associations, and weather patterns) in the southern Appalachians, we clustered our individual collection localities into seven general physiographic regions. These included the Cumberland Plateau (18 sites) and Ridge and Valley (11 sites) regions of western Georgia, the Cohutta-Rich Mountain complex (10 sites), at the southern limit of the Blue Ridge in Georgia, the transition zone between the Blue Ridge Escarpment and Upper Piedmont of Georgia and South Carolina (47 sites), the Blue Ridge of Georgia (21 sites), the Blue Ridge of North Carolina (28 sites), and the Chattooga River Basin (55 sites). We tested the possibility that abundance of *S. hoyi* would be negatively correlated with high abundance of more common, small-bodied soricids, *S. cinereus,* the masked shrew, or *S. longirostris,* the southeastern shrew, following Fox and Kirkland (1992), by Pearson product-moment correlation of capture rates of *S. hoyi* with those of *S. cinereus* and *S. longirostris.*

At 13 Blue Ridge province sites in Georgia (four cove-hardwood, five upland-hardwood, three white pine-hemlock riparian, and one newly regenerated mixed pine-hardwood), we assessed microhabitat parameters at each pitfall trap to determine microhabitat features associated with relative abundance of *S. hoyi.* At each trap, we noted elevation, aspect, slope (see above), type of trap cover (i.e., rock, log, etc.), condition of trap cover (degree of decomposition of logs on a scale of 1-3 with 1 being little decomposed and 3 being well decomposed), height of cover, length of cover, diameter at breast height (DBH) of trees nearest trap, distance to nearest suitable cover, condition of neighboring cover, number of herbaceous taxa within a 2-m radius of trap, percentage of leafcover within a 2-m radius of trap (ocularly estimated), and percentage of herbaceous cover within a 2-m radius of trap. At three locations at each site, measures of basal area were recorded with a two-factor, basal-gauge prism and percentage canopy cover was determined with a spherical densiometer. All microhabitat data were then averaged for each site. Pearson product-moment correlations were performed on means of all collected microhabitat variables against total number of *S. hoyi* caught per total number of trap nights and with total number of *S. hoyi* caught per trap per trapping period averaged for each of the 13 sites.

RESULTS

In 213,900 trap nights, we collected 261 *S. hoyi* at 102 (53%) of our 190 sites. Abundance, based upon captures/100 trap nights, was not well correlated with elevation (*r* = -0.140, *P* = 0.133, *n* = 190), slope (*r* = -0.164, *P* = 0.054, *n* = 89), or aspect (*r* = 0.068, *P* = 0.498, *n* = 103). Mean rates of capture/100 trap nights by habitat type and physiographic region are presented in Tables 1 and 2. Mean rates of capture ranged from a high of 0.257 in riverine-corridor sites to a low of 0.089 in white pine-hemlock; however, no significant difference in relative abundance was detected among habitat types (*F* = 0.65, *d.f.* = 6,183, *P* = 0.691). We did find differences in relative abundance among physiographic regions (*F* = 4.10, *d.f.* = 6,183, *P* < 0.001). The mean rate of capture was greatest in the Ridge and Valley province (0.610/100 trap nights) and was significantly different from rates of capture of the physiographic regions, which ranged from 0.080 and 0.147. However, rates of capture among the remaining physiographic regions were not significantly different. Abundance of *S. hoyi* was not correlated with

Table 1.—*Mean captures/100 trap nights by habitat types for Sorex hoyi in the southern Appalachians. Mean captures not followed by the same letter differ* (P < *0.05).*

Habitat type	n	Total trap nights	Mean captures/100 trap nights	Standard error of mean captures
Northern hardwoods	15	18,708	0.134 A	0.038
Cove hardwoods	28	33,360	0.108 A	0.022
White pine-hemlock	29	30,343	0.089 A	0.025
Upland hardwoods	65	75,606	0.178 A	0.053
Mixed pine-hardwoods	33	36,663	0.152 A	0.052
Yellow pine	13	8,560	0.234 A	0.081
Riverine	7	10,660	0.257 A	0.167

Table 2.—*Mean captures of* Sorex hoyi*/100 trap nights in the southern Appalachians by land-type association. Mean captures not followed by the same letter differ* (P < *0.005).*

Land type	n	Total trap nights	Mean captures/100 trap nights	Standard error of mean captures
North Carolina Blue Ridge	28	26,422	0.102 B	0.021
Georgia Blue Ridge	21	32,960	0.124 B	0.028
Chattooga River Basin	55	49,052	0.131 B	0.025
Blue Ridge Escarpment and Upper Piedmont	47	51,741	0.147 B	0.039
Cohutta/Rich Mountain Complex	10	12,079	0.080 B	0.027
Ridge and Valley	11	5,434	0.610 A	0.291
Cumberland Plateau	18	36,212	0.109 B	0.039

rates of capture of other small, long-tailed shrews; *S. cinereus* (*r* = 0.055, *P* = 0.450, *n* = 190) or *S. longirostris* (*r* = 0.130, *P* = 0.079, *n* = 190). Calculated spatial, niche-breadth value was 4.65, largest of the eight species of shrews in the region (Laerm et al., in press).

Total number of *S. hoyi* caught per total trap nights and total number of *S. hoyi* caught per trap per trapping period were poorly correlated with height of cover, length of cover, distance to nearest suitable cover, condition of neighboring cover, percentage of herbaceous cover within a 2-m radius of trap, percentage of leafcover within a 2-m radius of trap, and number of herbaceous taxa within a 2-m radius of trap (Table 3). Significant negative correlations were observed for basal area, condition of trap cover, DBH of trees nearest trap, percentage of canopy cover, and slope (Table 3). Strong correlations with basal area, condition of trap cover, DBH of trees nearest trap, and slope can be attributed partially to the comparatively large number (eight) of *S. hoyi* recovered in the regenerated-pine-upland-hardwood site. For instance, basal area, DBH of trees nearest trap, and percentage of canopy cover for this individual stand were virtually zero because of its age. Condition of trap cover was good (the lowest value was zero), due to amount of newly downed tops and slash, and slope was fairly level. When this site was removed from correlation analysis, basal area, condition

Table 3.—*Correlation coefficients* (r) *and probability values* (P) *for microhabitat variables associated with capture of* Sorex hoyi *at 13 sites in the Georgia Blue Ridge.*

	Total number caught per total trap nights		Total number caught per trap per trapping period	
Habitat variable	*r*	*P*	*r*	*P*
Elevation	-0.097	0.541	0.059	0.711
Aspect	-0.250	0.111	-0.108	0.496
Slope	-0.548	0.054	-0.551	0.051
Degree of decomposition of logs	-0.519	0.069	-0.573	0.041
Height of cover	-0.027	0.931	-0.031	0.920
Length of cover	0.091	0.767	0.082	0.790
DBH of trees nearest trap	-0.581	0.038	-0.582	0.037
Distance to nearest cover	0.124	0.744	0.169	0.684
Condition of neighboring cover	-0.146	0.635	-0.154	0.615
Number of herbaceous taxa within 2-m radius of trap	0.148	0.637	0.160	0.602
Percentage of leafcover within 2-m radius of trap	-0.147	0.631	-0.158	0.606
Percentage of herbaceous cover within 2-m radius of trap	-0.168	0.538	-0.148	0.606
Basal area	-0.519	0.069	-0.516	0.071
Percentage canopy cover	-0.883	<0.001	-0.886	<0.001

of trap cover, and DBH of trees nearest trap, were no longer significantly correlated with total number of *S. hoyi* caught per total trap nights and total number of *S. hoyi* caught per trap per trapping period. Slope, while not significant, retained fairly high negative correlation coefficients with $r = -0.382$, $P = 0.221$, and $n = 12$ for total number of *S. hoyi* caught per total trap nights and $r = -0.394$, $P = 0.205$, and $n = 12$ for total number of *S. hoyi* caught per trap per trapping period. Consistent with that observation, three of the steepest sites sampled for microhabitat features accounted for no *S. hoyi.* Percentage canopy cover retained a significant negative correlation with total number of *S. hoyi* caught per total trap nights at $r = -0.675$, $P = 0.016$, and $n = 12$, and with total number of *S. hoyi* caught per trap per trapping period at $r = -0.687$, $P = 0.014$, and $n = 12$. Length of cover approached significance with positive correlations with total number of *S. hoyi* caught per total trap nights at $r = 0.484$, $P = 0.111$, and $n = 12$, and total number of *S. hoyi* caught per trap per trapping period at $r = 0.471$, $P = 0.122$, and $n = 12$, when the newly regenerated pine-upland-hardwood site was removed.

DISCUSSION

The presence of *S. hoyi* at 53% of our study sites indicates the species is widely distributed throughout the region surveyed. It is present in all vegetational community types, at all elevations, slopes, and aspects, and each of the physiographic regions as defined above. While individual sites may not have yielded any *S. hoyi,* nearby sites did. The abundance of *S. hoyi* did not vary significantly by vegetational community type. However, the comparatively lower numbers caught per trap night in high-quality, mesic habitats, such as cove hardwood, northern hardwood stands and white pine-hemlock communities suggest that these are less favorable to *S. hoyi.* This is indicated by the negative correlation we observed between percentage canopy cover and total number of *S. hoyi* caught per total trap nights and total number of *S. hoyi* caught per trap per trapping period at our 13 Blue Ridge microhabitat sites. Mesic, high-quality, cove hardwood and northern hardwood sites in the southern Appalachians tend to have an almost complete canopy cover in the overstory. Similarly, white pine-hemlock, riparian sites usually are covered in a dense midstory layer of rhododendron. However, we cannot be certain that lower trap success in these areas was due to microhabitat features, such as canopy cover or other factors, or competition with other long-tailed soricids, because these sites tended to have highest densities of other shrews, particularly *S. fumeus* and *S. cinereus* (Laerm et al., in press). In general, we found *S. hoyi* to be most abundant in moderate to xeric sites, where we recovered fewer other species of long-tailed shrews (Laerm et al., in press). It was most abundant in early successional stages, sites where we recovered the fewest of other species of soricids. This is reflected in significantly greater rates of capture reported from the Ridge and Valley province of Georgia, which is dominated by upland hardwoods, mixed pine-hardwood, and intensively managed yellow pine communities. However, the comparatively greater abundance of *S. hoyi* in the Ridge and Valley may be related to absence of *S. cinereus* and low abundance of *S. fumeus* (Laerm et al., 1995). While mean rates of capture of *S. hoyi* in the Blue Ridge-Upper Piedmont interface sites were not significantly different from those of the Blue Ridge province sites, these interface sites showed the second greatest absolute rate of capture. Like those in the Ridge and Valley, the Blue Ridge-Upper Piedmont interface sites also are dominated by upland hardwoods, mixed pine-hardwood, and intensively managed yellow pine communities, and are characterized by low relative abundance of *S. cinereus* and *S. fumeus.* However, unlike the Ridge and Valley sites, which exhibited low abundance of *S. longirostris,* the Blue Ridge-Upper Piedmont interface sites exhibited the greatest abundance of *S. longirostris* (Laerm et al., in press).

The broad geographic distribution of *S. hoyi,* its occurrence in a diversity of vegetational communities, and presence at essentially all elevations throughout the southern Appalachian highlands is reflected in the high niche-breadth value compared to that of other regional soricids. Niche-breadth value for *S. hoyi,* based on our 190 sites, was 4.65 compared to niche-breadth values reported by Laerm et al. (in press) at 109 Blue Ridge sites for *Blarina brevicauda* (4.45), *S. fumeus* (4.17), *S. longirostris* (2.29), *S. cinereus* (2.14), *S. palustris* (2.00), *S. dispar* (2.00), and *Cryptotis parva* (1.20).

Summary of distributional records and habitat associations of S. hoyi winnemana.—New distributional records indicate that the range of the pygmy shrew is much more extensive than previously believed. A single specimen from Wabash Co., Illinois, was referred to *S. h. winnemana* by Diersing (1980) and Hoffmeister (1989). Although not known to occur in Indiana prior to Caldwell et al. (1982) and Cudmore and Whitaker

(1984), *S. h. winnemana* is now known from numerous localities in the southern unglaciated, forested portions of the state, including Perry, Dubois, Crawford, Harrison, Orange, Washington, Clark, Jackson, Lawrence, Monroe, Owen Brown, and Bartholomew counties (J. O. Whitaker, Jr., pers. comm.). Baird (1857) described a skin and mutilated skull from Zanesville, Muskingham Co., Ohio, which Diersing (1980) referred to *S. h. winnemana.* Svendsen (1976) reported three specimens taken from Zaleski State Forest, Vinton Co., Ohio, in 1975. Based on Diersing (1980), these would be referable to *S. h. winnemana* as well.

The single record of a pygmy shrew taken from the stomach of a red fox *(Vulpes vulpes)* in Potter Co., Pennsylvania, reported in H. R. Roslund (in litt.) and Doutt et al. (1966) proved to be *S. cinereus* (Diersing, 1980; Genoways, 1985). The recent occurrence of *S. hoyi* in Pennsylvania remained undocumented until it was reported from two localities, Center and Franklin counties, by Kirkland et al. (1987), who referred these specimens to *S. h. thompsoni.* More recently, Kirkland and Krim (1990) and Kirkland and Sheppard (1994) report on additional specimens obtained from Berks, Clearfield, Cumberland, Huntingon, and Westmoreland counties. Laerm et al. (1994a) reported a specimen from Fayette Co. in western Pennsylvania and referred it to *S. h. thompsoni.* Additional specimens are now known from elsewhere in Pennsylvania (G. L. Kirkland, Jr., M. A. Steele, and D. A. Schlitter, pers. comm.) and apparently are referable to *S. h. thompsoni.*

Until recently, there were only two documented occurrences of the pygmy shrew in Maryland; Prince George's Co. (Paradiso, 1966) and another from Baltimore Co. (Lee, 1974). Kirkland et al. (1987) examined the specimens from Maryland and referred the specimen from Prince George's Co. to *S. h. winnemana* and the specimen from Baltimore Co. to *S. h. thompsoni.* Three additional specimens recently were reported from Garrett Co. by Laerm et al. (1994a) and referred to *S. h. winnemana.*

About 25 records are now known from West Virginia, including Fayette, Monroe, Raleigh, Randolph, and Summers counties in the central and southern portion of the state, and Berkeley Co. in the eastern panhandle (B. Sargent, pers. comm.). Until recently, the pygmy shrew was considered rare in Virginia. Handley and Patton (1947) reported the species from two localities; Fairfax Co. (the type locality) and Campbell Co. Handley et al. (1980) reported it from additional localities in Prince William, Richmond, Surrey, Prince Edward, and Rockbridge counties. More recent reports by Pagels (1987), Pagels et al. (1992), Kalko and Handley (1993), and Mitchell et al. (1993) document records in Essex, King George, Campbell, Charlotte, Cumberland, Pittsylvania, Prince William, Allegheny, Augusta, Bath, Highland, Rockbridge, Wythe, and Dickeson counties. Pagels (1987) comments that the pygmy shrew is not only widely distributed in Virginia, occurring in the Coastal Plain, Piedmont, Ridge and Valley, and Appalachian Plateau provinces, but it also is known from a wide range of habitats and a considerable range in elevation. Despite its apparent wide distribution in Virginia, Pagels (1987) suggests the pygmy shrew is uncommon, indicating that in 21 of the 23 collection sites known to him, its occurrence is represented by only a single specimen.

Until recently, the species was known from a single specimen from Kentucky collected in 1903; however, no specific locality is available (Barbour, 1956; Barbour and Davis, 1974). More recently, Caldwell (1980), Caldwell and Bryan (1982), Bryan (1991), and Feldhamer et al. (1993) report on the occurrence of the pygmy shrew from 14 counties in the eastern portion of the state (Bath, Bell, Bowman, Breathitt, Greenup, Harlan, Jackson, Leslie, Letcher, Menifee, Pike, Rockcastle, Wayne, Wolfe), as well as three counties in west-central Kentucky (Breckenridge, Ohio, Warren), and further west in the area of Land Between the Lakes (Lyon and Triggs counties). H. Bryan (pers. comm.) informed us that he has taken the species in pitfall surveys in essentially every county in eastern Kentucky.

The pygmy shrew was first reported in Tennessee by Kennedy et al. (1979) when two specimens were taken in Monroe Co. Subsequently, Kennedy and Harvey (1980), Tims et al. (1989), M. J. Harvey et al. (in litt.), and Feldhamer et al. (1993) reported it from widely scattered localities in the eastern (Monroe and Polk counties), central (Grundy, Perry, and Van Buren counties), and western portions (Stewart Co.) of Tennessee.

The first records for North Carolina were two individuals reported by Jackson (1928) from Bent Creek Experimental Forest in Pisgah National Forest, Buncombe Co. Webster (1987) indicated that these latter specimens were erroneously reported from Translyvania Co. by E. R. Smith et al. (in litt.), Diersing (1980), and Lee et al. (1982). Subsequently, Hoffmeister (1968) reported a specimen from Newfound Gap, Swain Co.

Additional specimens are now known from the Dismal Swamp, Camden Co. (Rose and Padgett, 1994), and from Avery, Cherokee, Clay, Graham, Jackson, Macon, and McDowell counties in the Blue Ridge province (Laerm et al., 1994b).

Records for Georgia historically were restricted to Rabun Co. (Wharton, 1968), but Ford et al. (1994) reported them throughout the Blue Ridge province. The species was only recently reported from Oconee, Greenville, and Pickens counties, South Carolina (J. Laerm, in litt.; Mengak et al., 1987), and Jackson Co., Alabama (Laerm et al., 1996).

As indicated by our surveys, the pygmy shrew occurs in a variety of habitats throughout the southern Appalachian highlands. This is reflected in the available habitat data provided by other authors as well. For example, in South Carolina, Mengak et al. (1987) reported it from mature mixed pine-hardwoods, loblolly pine plantations, and hemlock-hardwood stands. Webster (1987) in North Carolina and Pagels (1987) in Virginia reported the species from higher elevations near fast-moving, mountain streams associated with the interface of northern hardwood and Appalachian montane-boreal forest, both with and without rhododendron understory. In southwestern Tennessee, Kennedy et al. (1979) reported the pygmy shrew from a small forest clearing at 1,325 m in northern hardwood community characterized by beech *(Fragus grandifolia),* maple, buckeye, and hawthorn *(Crataegus).* M. J. Harvey et al. (in litt.) collected the species in eastern Tennessee at elevations ranging as low as 400 m to as high as 1,525 m encompassing almost the entire spectrum of forest communities in the Cherokee National Forest. These habitat types included dry stands of white pine, upland hardwood, and Table Mountain pine, sites with moderate white oak and northern red, more mesic stands of cove hardwoods, higher-elevation northern hardwoods, and stands of red spruce-Fraser fir *(Picea rubens-Abeis fraseri).* Collections from mountainous regions of eastern Kentucky were associated with mixed mesophytic and streamside-forest stands, with an abundance of rock outcrops and fallen logs (Caldwell, 1980; Caldwell and Bryant, 1980).

Outside the southern Appalachians, the pygmy shrew was reported from the Piedmont of Virginia in oldfield and young clearcut areas dominated by early successional grasses, goldenrod *(Solidago),* and blackberry *(Rubrus),* and in mixed pine-hardwood sites of shortleaf pine and sweetgum (Pagels, 1987; Pagels et al., 1992). It also was taken in saturated forested wetlands in the Great Dismal Swamp of the Coastal Plain in both Virginia (Mitchell et al., 1993) and North Carolina (Rose and Padgett, 1994). Similarly, records from the Western Highland Rim and Upper Coastal Plain of Tennessee and Kentucky (Bryan, 1991; Feldhamer et al., 1993; Tims et al., 1989) included collections from a diversity of mixed-upland and bottomland-hardwood types, as well as young clearcuts.

Clearly, *S. h. winnemana* has a much wider geographic distribution than believed previously. It is reported from a considerable diversity of vegetational communities and elevations. With the possible exception of *S. longirostris, S. hoyi* is the most widely distributed long-tailed soricid in the southeastern United States. However, in comparison with *S. longirostris,* it occupies a much greater elevational distribution (Laerm et al., in press).

The comparatively rarity of *S. hoyi* compared to other soricids at all of the sites in which it has been collected is not clearly understood. Kirkland (1991), Fox and Kirkland (1992), and Kirkland and Sheppard (1994) suggest that multiple-species communities of soricids may be characterized by a species-assembly rule in which the three body-size niches (small, medium, large) should be filled before a second species of the same size is present. This may explain the relative rarity of *S. hoyi* throughout much of the southern Appalachian highlands. For example, we found *S. cinereus* to be the dominant small-bodied, long-tailed soricid throughout the Blue Ridge (Laerm et al., in press). This observation also is reported in other studies in the southern and central Blue Ridge, such as those of M. J. Harvey et al. (in litt.) in eastern Tennessee, Caldwell (1980) in Kentucky, Pagels and Tate (1976), Kalko and Handley (1993), and Pagels et al. (1994) in Virginia, and Kirkland and Sheppard (1994) in Pennsylvania.

At lower-elevation sites in the Georgia Piedmont, we found *S. longirostris* to be the dominant, small, long-tailed soricid. Here, we recovered no *S. hoyi.* Similarly, at low-elevation (<790 m) sites in the Blue Ridge province where we took *S. longirostris,* we recovered fewer *S. hoyi.* Similar observations were made in forested and clearcut habitats in the Virginia Piedmont (Pagels et al., 1993) and wetlands of the Dismal Swamp in southeastern Virginia (Mitchell et al., 1993). Contrary to these observations, in western Kentucky and Tennessee, Feldhamer et al. (1993) reported greater numbers of *S. hoyi* captured in their pitfall sites compared to *S. longirostris.*

Comments on conservation and taxonomic status of

S. h. winnemana.—Historically, *S. h. winnemana* has been afforded protection in several states in which it occurs, due to its relative rarity. It also was proposed for federal protection. However, because the species is so widespread and known from such a wide range of vegetational community types, there seems little justification for including the species as a candidate for endangered, threatened, or rate status under either federal or state guidelines throughout its range.

The new records of *S. h. thompsoni* from Pennsylvania reported by Kirkland et al. (1987) and Kirkland and Sheppard (1994) indicate that the supposed distributional gap between *S. h. winnemana* and *S. h. thompsoni* suggested by specimens available to Diersing (1980) probably do not exist, at least not in Pennsylvania. This was reinforced by G. L. Kirkland, Jr. and M. A. Steele (pers. comm.) who collected additional specimens of *S. hoyi* (presumably *S. h. thompsoni)* in northeastern Pennsylvania. In addition, the new records reported by Laerm et al. (1994a) from western Maryland and Pennsylvania indicate a continuous distribution of *S. hoyi* occurring throughout the southern and central Appalachians into Pennsylvania and northward. We suggest that a reevaluation of the *S. h. winnemana*-thompsoni complex in the eastern United States may well indicate that pygmy shrews in this region represent a continuous cline of increasing size from south to north. If such is the case, the taxonomic distinction of *S. h. winnemana* would be questionable.

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RADIOTELEMETRIC ASSESSMENT OF MOVEMENT PATTERNS OF THE GRAY BAT (*MYOTIS GRISESCENS*) AT GUNTERSVILLE RESERVOIR, ALABAMA

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We used radiotelemetry to study seasonal variation in movement patterns of gray bats *(Myotis grisescens)* at Guntersville Reservoir, Alabama. Individual gray bats foraged over large areas of Guntersville Reservoir, and there was considerable movement of bats between Blowing Wind and Hambrick caves. Average minimum size of home range of individual gray bats at Guntersville Reservoir was 97 km^2. Bats may have had a greater affinity for foraging areas during and shortly after young became volant, and during the breeding season than later in the active season as time to enter hibernation neared. Bats moved over a broader area when young became volant than later in the active season. Greatest number of days a bat was detected at the same monitoring site, greatest distances traveled by bats, and greatest number of nights a bat was found at the same locality did not vary between sampling periods. During 1991, gray bats were detected more often at about the time young became volant than later in the active season.

The gray bat *(Myotis grisescens)* has a limited distribution in limestone-karst areas of the eastern and southern United States (Hall, 1981; Hall and Wilson, 1966; Rabinowitz and Tuttle, 1980). Primarily because of habitat destruction and molestation by humans (Barbour and Davis, 1969; Tuttle, 1979a, 1979b), the gray bat was listed as an endangered species by the United States Fish and Wildlife Service (Greenwalt, 1976). Large winter colonies of the gray bat hibernate in only nine caves. In early spring, winter colonies disband and leave winter hibernacula. Adult females emerge from hibernation first, followed by yearlings of both sexes, and finally by adult males. Bats move to other caves where they form large transient colonies that occupy caves for several days. Gray bats then form maternity colonies, where females give birth and raise their young, and bachelor colonies, which predominantly contain males and non-reproductive females. After young become volant, sex and age segregation weakens. Young-of-the-year of both sexes remain with females in maternity colonies during July and August. Autumn migration takes place in the same order as spring emergence, with adult females leaving in early September and young-of-the-year remaining behind with the last males to leave, usually by mid-October (Elder and Gunier, 1978; Tuttle, 1976a, 1979a).

Movement patterns among summer caves and between summer caves and hibernacula, are relatively well understood (Elder and Gunier, 1978; Hall and Wilson, 1966; Tuttle, 1976a, 1979a). Gray bats generally occur as discrete populations that occupy a series of summer caves associated with one or a few hibernacula (Elder and Gunier, 1978; Hall and Wilson, 1966; Tuttle, 1976a). However, affiliation between summer caves and winter hibernacula also may involve long-distance movements by a few individuals (Elder and Gunier, 1978; Hall and Wilson, 1966; Tuttle, 1976a) or by whole populations. Gray bats from northwestern Florida, for example, regularly migrate to a winter hibernaculum in northeastern Alabama (Tuttle, 1976a).

During summer months, Blowing Wind and Hambrick caves, located at Guntersville Reservoir in northeastern Alabama, contain the two largest summer colonies of gray bats (Tuttle, 1976a; United States Fish and Wildlife Service, in litt.). The combined populations of gray bats at Blowing Wind and Hambrick caves is ca. 600,000, a doubling of their population during the past 10 years (The Tennessee Valley Authority, in litt.). Blowing Wind Cave (primarily a bachelor colony) and Hambrick Cave (a maternity colony) contain bats that represent a single colony, and almost all of the bats from this association hibernate in nearby Fern Cave. Bats banded in Hambrick Cave have been found hibernating only in Fern Cave, but recoveries of hibernating bats banded at Blowing Wind Cave were more widely distributed. Most hibernated in Fern Cave, but some also hibernated in Tennessee and Missouri. Recoveries of banded bats of all sexes and ages for all times of the year from Blowing Wind Cave indicate movements throughout northern Alabama and middle Tennessee (Tuttle, 1976a).

Although large-scale movement patterns among caves inhabited by single colonies of gray bats are well documented, smaller-scale movement patterns are not well known. During the active season of gray bats, movement patterns associated with foraging require forays from summer caves. At Norris Reservoir, Tennessee, Rabinowitz (1978) found that gray bats foraged at some sites more than others; this foraging pattern may be correlated with abundance of prey species, e.g., mayflies (Ephemeroptera—Rabinowitz, 1978; Rabinowitz and Tuttle, 1982; Tuttle, 1976b). Gray bats may forage 15-35 km from the roost each night, and foraging activities are restricted to the local range of the population, which may be 50 km across (Tuttle, 1976a). Although night-flying, aquatic insects serve as the primary source of food for *M. grisescens,* little is known about foraging and movement patterns of gray bats in Alabama. Guntersville Reservoir is large and supports a variety of aquatic habitats, but not all regions of the reservoir provide equal quantities of acceptable prey species. Gray bats probably use a variety of foraging sites throughout the active season to optimize foraging effort. The only previous study of movement patterns of *M. grisescens* at Guntersville Reservoir was conducted during the 1960s and early 1970s, when the population of gray bats was decreasing (Tuttle, 1975, 1976a, 1976b, 1979a, 1979b).

Historically, various methods have been used to study biology and movement patterns of *M. grisescens.* Banding and recovery has been the method most widely employed (Elder and Gunier, 1978, 1981; Gunier and Elder, 1971; La Val et al., 1977; Stevenson and Tuttle, 1981; Tuttle, 1975, 1976a, 1976b; Tuttle and Robertson, 1969; Tuttle and Stevenson, 1977), but this technique may involve capturing bats several times and it may be critically disturbing to a colony. At times, it has been necessary to use a shotgun to sacrifice bats to recover bands (Tuttle, 1976b). Attached chemiluminescent capsules make dispersing *M. grisescens* more easily detectable, and when observed from a helicopter, the bats can be followed with relative ease (La Val et al., 1977). Observations using night-vision equipment also have been successful (Rabinowitz, 1978). Because they are swift fliers (18-39 km/h—Kennedy and Best, 1972; La Val et al., 1977; Tuttle, 1976a), gray bats can disappear from sight quickly, but radiotelemetry eliminates the need to maintain visual contact with the bats. Technology to monitor movements of small bats by radiotelemetry was not available in the 1960s and 1970s when most studies of *M. grisescens* were conducted in Alabama. Radiotelemetry may provide answers to questions about foraging ecology and movement patterns of this species, and reveal additional information that will be useful in its protection and management. The objective of our study was to use radiotelemetric monitoring to elucidate seasonal variation in movement patterns of individual *M. grisescens* at Guntersville Reservoir.

METHODS AND MATERIALS

This study was conducted at Guntersville Reservoir, a 27,479-ha impoundment of the Tennessee River in northeastern Alabama and southern Tennessee. The reservoir was constructed ca. 50 years ago for commercial navigation, flood control, and hydroelectric generation. It is bounded downstream by Guntersville Dam and upstream by Nickajack Dam in Tennessee. The area surrounding Guntersville Reservoir consists of a mixture of pine-hardwood forests and open pastures. Limestone caves suitable for *M. grisescens* are situated near the reservoir and its tributary systems, and three caves, Blowing Wind, Hambrick, and Nickajack, are used each summer by large colonies of gray bats. Two of these caves, Nickajack (located on Nickajack Reservoir, Tennessee) and Hambrick, open directly onto the water, but Blowing Wind Cave is separated from the reservoir by a distance of ca. 100 m. Entrances of these three caves have been fenced or gated to prevent disturbance of bats by humans.

During summer 1991 (8 July-17 September), gray bats were captured using a harp trap (Tuttle, 1974) as they emerged from Blowing Wind Cave, Jackson Co., Alabama, and in summer 1992 (9 July-14 September) as they emerged from Blowing Wind Cave and Hambrick Cave, Marshall Co., Alabama. Bats were aged as young-of-the-year or adult; young-of-the-year were differentiated by prominent vascularization present at the wrist (Anthony, 1988; Barbour and Davis, 1969). While most females in the population of gray bats at Guntersville Reservoir gave birth and raised their young at Hambrick Cave, a nursery colony containing >2,000 young also was present in Blowing Wind Cave; mothers of these young-of-the-year were the primary focus of research efforts.

Radiotransmitters were attached to 6 adult males and 21 post-lactating, adult females in 1991 and to 34 post-lactating, adult females in 1992. Hair was partially removed from a 1-cm^2 area on the back with scissors, and a radiotransmitter (0.8 g, model BD-2A with reed switch, Holohil Systems Ltd., Carp, Ontario, Canada) was attached using non-toxic, Skin-Bond Cement (Smith and Nephew United, Inc., Largo, FL). Transmission distance for these radiotransmitters is ca. 3-5 km, but may be >10 km over open water with no physical obstructions. No apparent distress was caused to bats by these procedures.

Five teams of two persons each monitored bats throughout the night (1930-0600 h CDT) using TRX-2000S radioreceivers (Wildlife Materials, Inc., Carbondale, IL) and collapsible three and five-element Yagi antennae. When possible, walkie-talkies were used to communicate among teams of observers concerning movements of individual bats. During 1991, bats were monitored from >30 sites, the number and location of which varied throughout summer (Fig. 1; sites 1-12). In 1992, the number of monitoring sites was reduced to seven (Fig. 1; sites 1, 2, 8, 9, 12, 13, and 14), chosen for their wide vantage points and because information gathered in 1991 indicated that these were areas frequently used by bats. Each radiotransmitter frequency usually was monitored on a 1-min rotational basis throughout the night. As in 1991, five teams of two observers each monitored bats throughout the night. The entrance of Blowing Wind Cave was monitored throughout all sampling periods in 1991 and 1992.

Six parameters were used to assess movement patterns, roost fidelity, and home ranges of individual bats. To provide an estimate of how long individual bats remained in the vicinity of Guntersville Reservoir, we examined number of days between receipt of the first and last radiotransmission from a bat and number of successful attempts to locate each bat. To provide an estimate of size of home range, roost-site fidelity, and foraging-site fidelity, we examined total number of sites where each bat was located, number of times each bat was located (i.e., ≥15 min between each time the bat was detected), greatest distance each bat traveled from where the radiotransmitter was attached (measured along a straight line in kilometers), and greatest number of nights each bat was found at the same locality. To assess variation of these parameters within years, we divided each year into early and late-season sampling periods (8 July-5 August and 19 August-3 September in 1991, 9 July-7 August and 21 August-4 September in 1992, respectively). The early season sampling period generally corresponded to when young became volant and to the premigratory time for adult females, and the late-season period generally corresponded to when adult females began to migrate to hibernacula, the time of copulation, and to the premigratory time for young-of-the-year and adult males (Tuttle, 1975, 1976a, 1976b). One-way analysis of variance was used to assess differences between sexes and sampling periods. To provide an estimate of minimum size of home range of individual bats, we plotted localities where bats with radiotransmitters were detected, connected the points with straight lines, measured the greatest length and width (90° to length) of home range, and overlaid a grid to estimate minimum area of the home range. All statistical analyses were conducted using SPSS/PC+ (Norŭsis, 1990).

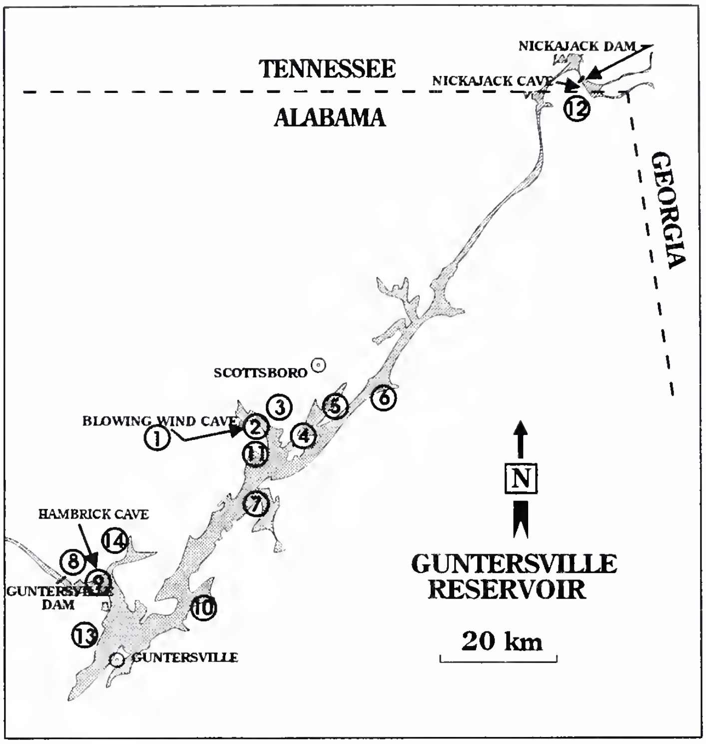

Fig. 1.—Sites monitored for gray bats *(Myotis grisescens)* at Guntersville Reservoir, Alabama, and Nickajack Reservoir, Tennessee: 1) Blowing Wind Cave; 2) Jackson County Highway 114 (south of US Highway 72); 3) Island in North Sauta Creek; 4) Goose Pond Colony (boat ramp); 5) Jackson County Sportsman's Club (boat ramp); 6) B. B. Comer Bridge (boat ramp); 7) South Sauta Creek (boat ramp); 8) Guntersville Dam; 9) Hambrick Cave; 10) Guntersville State Park; 11) Mink Cove; 12) Nickajack Cave; 13) Brown's Creek; 14) Honeycomb Creek Campground. In addition, 16 other sites were monitored at irregular intervals.

RESULTS

During 1991, 38,771 attempts (81,452 min) were made to locate the 27 bats with radiotransmitters attached to them (Table 1). Unknown electrical sources near monitoring sites interfered with radiotransmissions at some lower frequencies (150.000-150.300 KHz). Consequently, data for 11 bats were omitted from analyses. Of the remaining 16 bats, radiotransmissions were received from 10 of them (three males, seven females), and six (three males, three females) were not located after release. Activity areas of bats generally were near Blowing Wind and Hambrick caves. Of the 10 bats detected after release, six remained within 10 km of Blowing Wind Cave, one (150.578) was located ca. 20 km downstream at Guntersville State Park, and three (150.370, 150.418, 150.517) were located in the Hambrick Cave-Guntersville

Table 1.—*Gender of gray bats* (Myotis grisescens), *frequency of radiotransmitter (KHz), date radiotransmitter was attached, date of receipt of last radiotransmission, total number of attempts to locate the bat, number of minutes spent attempting to locate the bat, and number of minutes the bat was located at Guntersville Reservoir, Alabama, 1991-1992. Radiotransmitters were attached to bats at Hambrick (indicated by an asterisk) and Blowing Wind caves.*

Year	Gender of bat	Transmitter frequency	Begin date	End date	Number of attempts	Minutes attempted	Minutes located
1991	F	150.458	8 Jul	10 Jul	225	1,068	40
	F	150.016	9 Jul	N/A	3,176	9,590	N/A
	F	150.038	22 Jul	N/A	2,101	4,925	N/A
	F	150.418	22 Jul	14 Aug	1,927	5,212	43
	F	150.138	22 Jul	N/A	2,103	4,972	N/A
	F	150.080	23 Jul	N/A	2,047	4,997	N/A
	F	150.157	19 Aug	N/A	714	1,359	N/A
	F	150.178	5 Aug	N/A	1,396	2,836	N/A
	F	150.057	5 Aug	N/A	1,428	2,892	N/A
	F	150.247	5 Aug	N/A	1,490	3,061	N/A
	F	150.266	5 Aug	N/A	1,469	3,062	N/A
	F	150.308	5 Aug	N/A	2,234	6,499	N/A
	F	150.370	5 Aug	14 Aug	2,322	4,167	4
	F	150.220	19 Aug	N/A	844	1,636	N/A
	F	150.349	19 Aug	19 Aug	1,809	2,889	0
	M	150.756	19 Aug	19 Aug	1,657	2,669	0
	M	150.398	19 Aug	23 Aug	1,687	2,728	8
	M	150.439	19 Aug	19 Aug	677	1,341	0
	F	150.328	23 Aug	23 Aug	592	1,912	0
	F	150.497	3 Sep	3 Sep	1,413	2,284	1
	F	150.517	3 Sep	6 Sep	1,365	2,040	14
	F	150.578	3 Sep	7 Sep	1,417	2,289	1
	F	150.657	3 Sep	4 Sep	1,368	2,016	9
	F	150.697	3 Sep	3 Sep	1,368	2,036	0
	M	150.738	3 Sep	18 Sep	1,403	2,109	10
	M	150.637	17 Sep	17 Sep	270	431	0
	M	150.537	17 Sep	18 Sep	269	432	2
Total					38,771	81,452	132

Dam area, ca. 30 km from the release site (Thomas, 1994).

In 1991, four bats with radiotransmitters were detected on two or more occasions at the same monitoring site (Table 2), indicating that bats may have areas where they regularly forage (i.e., an individual home range). Data obtained in 1991 indicated that average home range of individual bats was ca. 4 by 17 km and covered an area of ca. 50 km^2 (Table 2). Generally, home ranges of the

Table 1.—*continued*

Year	Gender of bat	Transmitter frequency	Begin date	End date	Number of attempts	Minutes attempted	Minutes located
1992	F	172.650	9 Jul	15 Jul	3,978	8,080	54
	F	172.550	9 Jul	15 Jul	3,949	8,048	25
	F	172.950	9 Jul	14 Jul	3,931	8,195	22
	F	172.888	9 Jul	15 Jul	3,902	7,997	5
	F*	172.849	11 Jul	27 Jul	3,162	3,468	88
	F	172.969	24 Jul	24 Jul	2,883	3,404	0
	F	172.770	24 Jul	9 Aug	2,267	2,790	40
	F	172.591	24 Jul	8 Aug	2,878	3,403	10
	F	172.691	24 Jul	29 Jul	2,221	2,744	26
	F	172.729	24 Jul	12 Aug	2,132	2,689	2
	F	172.809	24 Jul	7 Aug	2,898	7,177	5
	F	172.830	24 Jul	8 Aug	2,139	2,696	13
	F*	172.572	6 Aug	11 Aug	2,147	2,952	1
	F*	172.631	6 Aug	9 Aug	3,178	4,344	12
	F*	172.872	6 Aug	12 Aug	2,154	2,737	14
	F*	172.909	6 Aug	12 Aug	2,146	2,783	7
	F	172.927	7 Aug	7 Aug	1,955	2,735	0
	F	172.671	7 Aug	8 Aug	1,956	2,510	1
	F	172.791	7 Aug	9 Aug	1,878	2,431	9
	F	172.989	7 Aug	9 Aug	1,971	2,524	0
	F	172.382	21 Aug	21 Aug	1,636	1,895	0
	F	172.020	21 Aug	21 Aug	1,705	2,191	0
	F	172.109	21 Aug	21 Aug	1,719	2,199	0
	F	172.259	21 Aug	21 Aug	1,635	1,894	0
	F	172.540	21 Aug	21 Aug	1,636	1,899	0
	F	172.710	21 Aug	21 Aug	1,696	2,004	0
	F	172.751	21 Aug	21 Aug	1,701	2,015	0
	F	172.168	4 Sep	4 Sep	776	776	0
	F	172.211	4 Sep	4 Sep	442	442	0
	F	172.304	4 Sep	4 Sep	722	724	0
	F	172.353	4 Sep	4 Sep	722	722	0
	F	172.431	4 Sep	4 Sep	724	739	0
	F	172.501	4 Sep	4 Sep	876	876	0
	F	172.640	4 Sep	10 Sep	1,068	1,133	80
Total					67,885	103,216	414

four bats that showed greatest movement from Blowing Wind Cave coincided with the area between Blowing Wind and Hambrick caves and reflected movements between the two caves. Limited observations of these four bats indicated one-way movements from Blowing Wind Cave to Hambrick Cave and Guntersville State Park; none of these bats returned to Blowing Wind Cave (Thomas, 1994).

During 1992, 67,885 attempts (103,216 min) were made to locate the 34 bats with radiotransmitters (all females). Sixteen of these bats were not detected after release, but radiotransmissions were received from 18 of

Table 2.—*Number of times gray bats* (Myotis grisescens) *were located after release (≥15 min between each time of location), number of sites where they were located after release (does not include site of release), and estimates of minimum size of home range at Guntersville Reservoir, Alabama, 1991-1992.*

Year	Frequency of transmitter	Number of locations	Number of sites	Minimum size of home range		
				Length (km)	Width (km)	Area (km^2)
1991	150.370	2	2	29	3	44
	150.398	1	2	3	3	5
	150.418	12	6[a]	29	9	193
	150.458	3	7[a]	7	4	15
	150.497	1	1			
	150.517	5	3[a]	29	5	73
	150.537	1	1			
	150.578	1	1	22		
	150.657	3	3	5	1	3
	150.738	4	3[a]	11	2	11
Average		3.3	2.9	17.3	3.9	49.1
1992	172.550	9	2[a]	22		
	172.572	1	1			
	172.591	4	2	31	9	140
	172.631	8	2[a]	15	9	68
	172.640	15	1[a]	22		
	172.650	13	2[a]	22		
	172.671	1	1	28		
	172.691	5	2[a]	89	5	223
	172.729	2	1[a]	28		
	172.770	25	3[a]	31	16	248
	172.791	3	1[a]	22		
	172.809	5	2[a]	31	16	248
	172.830	10	3[a]	31	9	140
	172.849	3	2[a]	15	9	68
	172.872	8	3[a]	15	9	68
	172.888	5	1[a]			
	172.909	5	1[a]	15		
	172.950	5	3[a]	29	7	102
Average		7.1	1.8	27.8	9.1	134.6
Overall average		5.7	2.2	24.2	6.9	97.2

[a] Radiotransmissions received at the same site ≥2 nights.

them at least once after release (Table 1). Excluding the release site, no individual bat was located at more than three monitoring sites (Table 2). Greatest activity of bats occurred near Blowing Wind Cave, Hambrick Cave, and Guntersville State Park, with 15 of the 18 bats being found two or more times at the same monitoring site (Table 2). A functioning radiotransmitter, which had been placed on a bat at Blowing Wind Cave 2 days previously, was recovered from a cave in Guntersville State Park, indicating the bats used roost sites other than Blowing Wind and Hambrick caves.

Of the 13 bats found after they were released at Blowing Wind Cave in 1992, one (172.888) was detected only at Blowing Wind Cave, two (172.550 and 172.650) traveled to Guntersville State Park (ca. 20 km) and returned, and one (172.950) went to Guntersville State Park, back to Blowing Wind Cave, then to Brown's Creek and Guntersville State Park (Thomas, 1994). Once they left Blowing Wind Cave, none of the remaining nine bats with radiotransmitters were detected there again; two bats (172.591 and 172.770) went to Guntersville State Park and Brown's Creek, one (172.830) moved between Brown's Creek, Guntersville State Park, and Hambrick Cave, two (172.640 and 172.791) went to Guntersville State Park, two (172.671 and 172.729) went to Brown's Creek, one (172.809) went to Guntersville State Park, Brown's Creek, and Hambrick Cave, and one (172.691) that was released at Blowing Wind Cave on 24 July was located at Brown's Creek on 26 July and outside Nickajack Cave, Tennessee, on 28 and 29 July, ca. 75 km upriver from the capture site and >100 km from Brown's Creek (Fig. 1; Thomas, 1994). The five bats with radiotransmitters attached to them at Hambrick Cave were found only at the release site, Brown's Creek, and Guntersville State Park (Table 2; Thomas, 1994). Data obtained in 1992 indicated the average home range was ca. 9 by 28 km and covered an area of ca. 135 km^2. When combined with 1991 data, average minimum size of home range of gray bats at Guntersville Reservoir was ca. 7 by 24 km and covered an area of ca. 97 km^2 (Table 2).

When amount of effort made to locate bats in 1991 was examined statistically, there was no significant difference between the sampling periods of 8 July-5 August and 19 August-3 September for number of attempts to locate bats (*F*-value = 0.575, *d.f.* = 1,14, $P = 0.461$; 8 July-5 August, $n = 3$, $\bar{x} = 1{,}491$ attempts/bat, range = 225-2,322; 19 August-3 September, $n = 13$, $\bar{x} = 1{,}177$ attempts/bat, range = 269-1,809), but there was a significant difference between sampling periods for number of minutes spent attempting to locate bats in 1991 (*F*-value = 4.927, *d.f.* = 1,14, $P = 0.044$; 8 July-5 August, $n = 3$, $\bar{x} = 3{,}482$ min attempted/bat, range = 1,068-5,212; 19 August-3 September, $n = 13$, $\bar{x} = 1{,}937$ min attempted/bat, range = 432-2,889). For 1992, there were significant differences between sampling periods for number of attempts to locate bats (*F*-value = 40.202, *d.f.* = 1,32, $P \leq 0.001$; 9 July-7 August, $n = 20$, $\bar{x} = 2{,}686$ attempts/bat, range = 1,955-3,978; 21 August-4 September, $n = 14$, $\bar{x} = 1{,}218$ attempts/bat, range = 442-1,719) and number of minutes spent attempting to locate bats (*F*-value = 20.143, *d.f.* = 1,32, $P \leq 0.001$; 9 July-7 August, $n = 20$, $\bar{x} = 4{,}185$ min attempted/bat, range = 2,431-8,195; 21 August-4 September, $n = 14$, $\bar{x} = 1{,}394$ min attempted/bat, range = 442-2,199). Thus, subsequent analyses of the six parameters used to assess movement patterns were conducted after data recorded for each bat were divided by number of minutes we attempted to locate the bat, then multiplied by 100.

Statistical analyses of number of days between receipt of first and last radiotransmission indicated no significant differences between sexes or between sampling periods during 1991. However, in 1992, number of days that radiotransmissions were received was significantly greater in the 9 July-12 August sampling period than in the 21 August-10 September period (Table 3). Thus, bats remained in the vicinity of monitoring sites for more days in the sampling period of 9 July-12 August than 21 August-10 September 1992. These bats may have a greater affinity for foraging areas during and shortly after the time young become volant and during the breeding season than later in the active season as time to enter hibernation nears.

In 1991, number of successful attempts to locate a bat did not differ between sexes, but a significant difference was present between sampling periods; there was a greater number of successful attempts to locate bats for 8 July-14 August than for 19 August-18 September (Table 3). There was no significant difference between sampling periods in 1992. Thus, during 1991, bats were found more often at about the time young became volant than later in the active season. Bats tended to lose affinity for foraging areas after young become volant.

Number of sites where a bat was detected after release did not differ between sexes, but in 1991 and 1992, there were significant differences between sampling periods (Table 3). In 1991 and 1992, bats were

Table 3.—*Results of one-way analysis of variance between sexes and times radiotransmitters were attached for variables examined in a radiotelemetric assessment of foraging patterns of gray bats* (Myotis grisescens) *at Guntersville Reservoir, Alabama, 1991-1992. One asterisk indicates* P ≤ *0.05 and two asterisks indicate* P ≤ *0.001.*

				Results of ANOVA		
Variable and date	*n*	$\bar{x}$	range	*d.f.*	*F*	*P*
Number of days between receipt of first and last radiotransmission/number of minutes attempted X 100						
1991						
Males	6	0.234	0-0.759			
Females	10	0.150	0-0.461	1,14	0.525	0.481ns
8 July-14 August	3	0.327	0.240-0.461			
19 August-18 September	13	0.148	0-0.759	1,14	1.661	0.218ns
1992						
9 July-12 August	20	0.240	0-0.744			
21 August-10 September	14	0.044	0-0.618	1,32	7.893	0.008*
Number of successful attempts to locate each bat/number of minutes attempted X 100						
1991						
Males	6	0.205	0-0.474			
Females	10	0.589	0-3.745	1,14	0.633	0.439ns
8 July-14 August	3	1.555	0.096-3.745			
19 August-18 September	13	0.189	0-0.686	1,14	7.781	0.015*
1992						
9 July-12 August	20	0.450	0-2.538			
21 August-10 September	14	0.504	0-7.061	1,32	0.015	0.904ns
Total number of sites where each bat was located/number of minutes attempted X 100						
1991						
Males	6	0.075	0-0.232			
Females	10	0.120	0-0.655	1,14	0.279	0.606ns
8 July-14 August	3	0.273	0.048-0.655			
19 August-18 September	13	0.064	0-0.231	1,14	5.043	0.041*

Table 3.—*continued*

				Results of ANOVA		
Variable and date	*n*	$\bar{x}$	range	*d.f.*	*F*	*P*
1992						
9 July-12 August	20	0.044	0-0.111			
21 August-10 September	14	0.006	0-0.088	1,32	12.770	0.001**
Number of times each bat was located/number of minutes attempted X 100						
1991						
Males	6	0.077	0-0.232			
Females	10	0.104	0-0.281	1,14	0.238	0.633ns
8 July-14 August	3	0.186	0.048-0.281			
19 August-18 September	13	0.072	0-0.245	1,14	3.181	0.096ns
1992						
9 July-12 August	20	0.152	0-0.896			
21 August-10 September	14	0.097	0-1.324	1,32	0.370	0.548ns
Greatest distance (km) each bat traveled from where radiotransmitter was attached/number of minutes attempted X 100						
1991						
Males	3	0.211	0-0.522			
Females	7	0.648	0-1.422	1,8	2.236	0.173ns
8 July-14 August	3	0.636	0.556-0.696			
19 August-18 September	7	0.466	0-1.422	1,8	0.271	0.617ns
1992						
9 July-12 August	17	0.746	0-3.243			
21 August-10 September	1	1.942	—	1,16	2.414	0.140ns
Greatest number of nights each bat was found at the same locality/number of minutes attempted X 100						
1991						
Males	6	0.107	0-0.463			
Females	10	0.045	0-0.098	1,14	1.112	0.310ns
8 July-14 August	3	0.071	0.024-0.096			
19 August-18 September	13	0.068	0-0.463	1,14	0.003	0.961ns
1992						
9 July-12 August	20	0.074	0-0.219			
21 August-10 September	14	0.025	0-0.353	1,32	3.300	0.079ns

more likely to be detected in the sampling periods of 8 July-14 August and 9 July-12 August, than in the sampling periods of 19 August-18 September and 21 August-10 September, respectively. In 1991, seven bats were detected beginning 19 August, but average number of sites was less than that for the three bats detected in the earlier sampling period (Table 3). Beginning 21 August 1992, only one bat was located after it was released (172.640). This bat was flying over the reservoir north (average direction from observers = 335°, range = 250-40°, where north = 360 and 0°) of the hotel facilities at Guntersville State Park and was detected at varying intervals during 0350-0440 h 7 September, 2013-2344 h 7 September, 0206-0448 h 8 September, 1945-2357 h, 2004-2126 h, and 2326-2400 h 9 September, and 2405-0308 h 10 September (Thomas, 1994). Thus, bats moved among more sites when young became volant than later in the active season. Bats moved over a broader area around the reservoir during earlier sampling periods.

There was no difference in number of times a bat was located after release, in greatest distance a bat traveled from where a radiotransmitter was attached, or in greatest number of nights a bat was found at the same locality, between sexes or between sampling periods during 1991 or 1992 (Table 3). Thus, number of times detected, greatest distances traveled, and greatest number of nights a bat was found at the same locality were similar throughout sampling periods.

DISCUSSION

It generally is assumed that addition of a radiotransmitter weighing 4-10% of body mass has a negligible effect on movement patterns of bats. Aldridge and Brigham (1988) demonstrated, however, that maneuverability decreased proportionally to increase in mass of radiotransmitter and recommended radiotransmitters ≤5% of body mass with animals <70 g. Because body mass of pregnant bats may increase >30%, an absolute upper limit of 30% was suggested, but this upper limit should be used only when food is abundant. Although the bat can forage with this load, its behavior will be modified (Aldridge and Brigham, 1988). Because body mass of gray bats we studied was 8-11 g, radiotransmitters (0.8 g) were ≤10% of body mass. Judging from distances bats traveled and length of time that radiotransmissions were received, bats apparently were unaffected by the radiotransmitters.

Based on earlier studies, the foraging range of *M. grisescens* was assumed to be <35 km (Tuttle, 1976a), and the majority of forays to be <12 km (range 1-35 km—La Val et al., 1977). Accordingly, monitoring sites were established around North Sauta Creek, a large, shallow-water tributary of Guntersville Reservoir, near the roost at Blowing Wind Cave (Fig. 1). Our initial plan was to maintain radiocontact among observers using walkie-talkies and attempt to triangulate locations of any bats detected, but this was not successful. During summer months, Blowing Wind Cave was home to 200,000-300,000 *M. grisescens* (The Tennessee Valley Authority, in litt.). Upon emergence from the roost, these bats dispersed in several directions, quickly moving out of sight and outside the range of radioreceivers. While many *M. grisescens* were observed foraging in the area of North Sauta Creek, a population density of this magnitude required many of the bats to forage in areas beyond the region of the reservoir being monitored. When an attempt was made to reconcile the situation by moving some of the monitoring sites farther away from the roost, we lost the ability to maintain radiocommunications with each other. The great distance between monitoring sites made attempts to triangulate the location of bats impossible.

M. D. Tuttle (in litt.) suggested that bats with radiotransmitters be followed by boat directly from the roost and observed with night-vision scopes to determine location and exact size of their territories, but this was not feasible. Blowing Wind Cave has two entrances, and neither opens directly onto the water. While most bats emerged from the largest entrance and went directly to North Sauta Creek, the nearest water, many bats flew overland at great heights for a distance of several kilometers to, presumably, broader expanses of Guntersville Reservoir. It would be nearly impossible to locate a specific bat at the cave entrance and follow it to its foraging territory, because bats frequently alternate between land and water in route to their destinations.

Most bats initially captured at Blowing Wind Cave remained in the vicinity of the cave in 1991 (Thomas, 1994). Gray bats tended to be transient, however, and more than one bat was detected near the Guntersville Dam-Hambrick Cave area, ca. 30 km away from Blowing Wind Cave. One bat was located near Guntersville State Park, ≥20 km from the capture site. There also is reason to believe that some bats traveled farther than shown by our data. During 1991, several bats with radiotransmitters were detected at Nickajack Cave, Tennessee, but because portions of the data became suspect when we discovered that false readings were being obtained on some of the lower radiofrequencies, the information was disregarded. Apparently, Tuttle (1976a) did not include Nickajack Cave, Tennessee, in his study of large-scale movement patterns of gray bats. However, our data indicate that Nickajack Cave probably is within the local range of the population that inhabits Blowing Wind and Hambrick caves, and most bats from Nickajack Cave likely hibernate in Fern Cave with other members of this population. Although bats from Nickajack Cave possibly hibernate elsewhere, none of 43 banded at Nickajack Cave, was recovered in the hibernating colony in Coach-James Cave, Edmonson Co., Kentucky (Hall and Wilson, 1966).

In addition to early or late migration, a few bats, most often yearlings or adults without young, may make lengthy trips to other places within their summer home range (Tuttle, 1976a). Gray bats apparently used alternate roost sites (Table 2). A monitoring team always was stationed at the capture site (i.e., Blowing Wind Cave), and we initially expected that bats with radiotransmitters would return to this site on a regular basis. However, they returned only sporadically or not at all. One bat from Blowing Wind Cave was recorded at Brown's Creek and at Nickajack Cave, Tennessee (ca. 75 km from the capture site and >100 km from Brown's Creek—Fig. 1; Thomas, 1994). This long-range movement pattern is consistent with other studies. An adult female *M. grisescens* from a colony in Tennessee was found 205 km distant on 7 August, at a cave outside the home range of the colony, and returned to the original colony site within 4 nights (Tuttle, 1976a), and bats in Kentucky also are known to travel ≤75 km between summer caves (Hall and Wilson, 1966).

There was further evidence that gray bats were using roost sites other than those where bats originally were captured. A radiotransmitter, which had been used in our study, was found in a cave at Guntersville State Park during summer of 1992. Tuttle (United States Fish and Wildlife Service, 1982, in litt.) suggested that gray bats were territorial, and depending on abundance of prey, foraging territories may be occupied by 1-15 bats. He also suggested that females in reproductive condition seemed to control these territories, which are located in the same places and used by the same bats year after year. If this assumption is true, *M. grisescens* probably is most territorial at critical times of the year, e.g., when it is caring for its young. During our study, which was conducted after young became volant each year, some bats repeatedly returned to the same foraging sites suggesting that gray bats have large individual home ranges (Table 2).

La Val et al. (1977) observed gray bats from a helicopter in Missouri and found that bats flew rapidly and directly to foraging areas. In most instances, the flight path of bats that flew cross-country took them over water again within a few minutes. Bats foraged over water, with brief forays into riparian vegetation. Gray bats they observed tended to be in groups of two or three adjacent to heavily wooded bluffs and hillsides. When subsequent passes were made along the river in the helicopter, foraging bats, assumed to be the same individuals, often were observed in the same places as on the previous pass (La Val et al., 1977). In Tennessee, Rabinowitz and Tuttle (1982) reported that gray bats sometimes fed continuously at feeding territories for several hours before returning to their roosts. Like La Val et al. (1982), we also found that bats tended to be concentrated in groups in foraging areas, but groups or individual bats rarely stayed >1 h before leaving. Based upon our radiotelemetry data, none of the bats continuously fed in any location for several hours. We suspect that Rabinowitz and Tuttle (1982) and La Val et al. (1982) observed different individuals or groups of bats that were passing through a foraging area instead of the same bats remaining for long periods to time. Qualitative observations of bats in foraging areas indicated that several bats foraged over the water followed by times when no bats were present. Our observations of short-term foraging times at particular sites by individuals or small groups of bats also are supported by observations of La Val et al. (1982) in Missouri. They reported that one female was followed by helicopter for 63 min on 19 May. During this time, she foraged continuously above the water along a 0.5-km section of the river. Occasional forays were made into riverbank trees, but these were of brief duration. She foraged from just above the water to treetop level, but most commonly remained 2-10 m above water. At the end of the observation period, she returned to the cave from which she had been released. Another female on 18 May was observed foraging for 21 min during which she flew at a height <2 m over water for much of the time, within a 0.6-km section of the river (La Val et al., 1977). We do not believe that individual bats returned to roost sites after short foraging forays, but we believe that foraging bats move on to foraging sites their predecessors have vacated. Because we never detected a bat in any foraging area for a long period of time in the same night, we believe that foraging areas were visited at irregular intervals throughout the night by different individuals or groups of bats. Further, individual bats may return to the same foraging site on subsequent nights and often at about the same time.

We have ascertained that 1) individual gray bats foraged over large areas of Guntersville Reservoir, 2) there was considerable movement of bats between Blowing Wind and Hambrick caves, 3) average minimum size of home range of individual gray bats at Guntersville Reservoir was ca. 7 by 24 km and covered an area of ca. 97 km^2, 4) bats may have a greater affinity for foraging areas during and shortly after young become volant and during the breeding season than later in the active season as time to enter hibernation nears, 5) during 1991, bats were found more often at about the time young became volant than later in the active season, 6) bats moved over a broader area during the time young became volant than later in the active season, and 7) greatest number of days at the same monitoring site, greatest distances traveled, and greatest number of nights a bat was found at the same locality did not vary between sampling periods. Further studies are needed to determine precise microhabitats that are most important to *M. grisescens* at Guntersville Reservoir. Data acquisition in our radiotelemetric study was limited because of great distances traveled by gray bats and inability to determine which microhabitats the bats were foraging over. Use of alternate techniques of study or modification of our radiotelemetric techniques, e.g., radiotelemetric monitoring with the aid of aircraft or satellites, or developing methods to quantify rates of visitation by bats to specific microhabitats, might prove to be more precise in determining specific microhabitats used by gray bats during their nightly forays.

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DISTRIBUTION AND STATUS OF LASIURINE BATS IN GEORGIA

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Specimen records for four species of lasiurine bats, genus *Lasiurus,* were examined for the state of Georgia. Published information about population status, habitat preferences, and roost locations of these species also was examined. We concluded that not enough specific information existed to produce models to predict effects of various forest manipulations on populations of lasiurine bats. Current growth and harvest trends for forests also were examined in Georgia. We predicted that roost habitat of lasiurines might decline in southeastern Georgia, but forests, particularly hardwoods, and potential habitats of lasiurines appeared to be increasing slightly in both area and age elsewhere in the state.

Following passage of the National Forest Management Act of 1976, which specified that all forest resources must be addressed in planning and management, comprehensive resource planning was implemented on most public and many private forests (Kirkland et al., 1986). Much emphasis in such management schemes was placed on developing models of how different forest-management strategies might impact certain animal taxa (e.g., Benson and Laudenslayer, 1986). Most models emphasize habitat types because many species of wildlife can be associated with certain habitat structure (e.g., Geibert, 1979; Heatwole, 1982; Karr, 1971; MacArthur et al., 1966; Martin, 1960; Maser et al., 1981; Rabenold, 1978; Short and Williamson, 1986). Some models focus on either specific taxa as indicator species or animal guilds (Block et al., 1986). The taxa used to develop most models have included mostly large mammals or songbirds. Bats rarely are considered in models, although they are important components of many forest systems and their populations can be impacted by forest-management activities (Thomas, 1988).

Development of wildlife-habitat models is dependent on knowledge about requirements of species, their responses to various habitat manipulations, and their interactions with environmental factors (Verner et al., 1986). However, our knowledge of how bats use and interact with forest ecosystems is in its infancy. Accurate estimations of population numbers, population trends, and geographic distributions are difficult to obtain for most species of bats (Tuttle, 1979). The most accurate information on population density and distribution are available for bats that roost in caves, mines, or buildings. Little is known about natural history, population status, or distribution of most species of bats that roost solitarily in tree hollows, under bark, or in foliage (Constantine, 1966).

For the purposes of this paper, we selected a taxon of foliage-roosting bats, the genus *Lasiurus,* and assessed what was known of distribution, population status, and habitat requirements of these bats in a single state, Georgia. We also examined various measures of forest systems in the state, such as trends in forest area and type. Our goal was to determine whether enough information was known about habitat requirements and distribution to model future trends in populations of bats under different forest-management strategies.

STUDY AREA

The state of Georgia encompasses 153,166 km^2 and is the largest state east of the Mississippi River. The state can be divided into five physiographic regions (two regions are small and occur only in the northern corners of the state), but with the exception of coastal salt marshes and grassy areas in Okefenokee Swamp, forests once covered the state (Nelson, 1957; Plummer, 1975). The potential natural vegetation of Georgia probably was an oak *(Quercus)* forest in the northeastern mountains and an oak-hickory-pine *(Quercus-Carya-Pinus)* forest in the northwestern mountains, the Piedmont, and the upper coastal plain (Kuchler, 1964). Except where southern floodplain forests of oak-gum-cypress *(Quercus-Nyssa-Taxodium)* occur along river bottomlands, major forest types in the lower coastal plain included longleaf-slash pine (*P. palustris* and *P. elliotti)* and loblolly-shortleaf pine *(P. taeda* and *P. echinata).*

Although the virgin forest was modified for centuries by Native Americans to increase production of wild food plants and to clear fields for agriculture (Stewart, 1956), extensive deforestation did not occur until the state was settled by Europeans. From the mid-1700s until the early 1920s, cotton was the dominant crop in Georgia, and most land in the Piedmont and coastal plain was converted from timber to agriculture (Brender, 1974). After invasion of the boll weevil *(Anthonomus grandis)* in the 1920s, large areas of cropland were abandoned and reverted to pine (primarily *P. taeda* and *P. echinata),* although nearly all of the original topsoil had been lost from most of the Piedmont and coastal plain uplands and gullying was extensive in the Piedmont (Odum and Turner, 1990).

During the past 2 decades, land-use patterns in Georgia have undergone considerable change. Although land area in farmland decreased in the state as a whole, it increased in the coastal plain. Forests now cover ca. 65% of the state, but forest area varies from ca. 85% in some mountain counties to 40% in many coastal plain counties (Odum and Turner, 1990). Despite a dramatic increase in the human population and urbanization, ground occupied by cities and towns in Georgia remains at only ca. 6% of the state's total land area.

METHODS AND MATERIALS

To determine known distribution of lasiurine bats in Georgia, specimen records in museums were examined by J. Laerm. Literature references to other locations of *Lasiurus* in the state also were studied. Occurrences of lasiurine bats were plotted on state maps by county. The literature was examined to locate references concerning population density or relative density and roosting habitats of *Lasiurus* in the state. Current trends in forest resources of the state (Cubbage et al., 1991) were compared to forest-roost preferences of each species as a means of projecting future population trends in lasiurine bats.

DISTRIBUTION AND STATUS OF BATS

Bats of the genus *Lasiurus* are among several species in Georgia that roost solitarily in trees or foliage. Four species of lasiurine bats occur in Georgia; the eastern red bat *(L. borealis),* Seminole bat *(L. seminolus),* hoary bat *(L. cinereus),* and northern yellow bat *(L. intermedius).* None of these bats show a known preference for either coniferous or deciduous trees as roost sites.

Lasiurus borealis.—Eastern red bats are found from southern Canada southward through the central and eastern United States and northeastern Mexico (Hall, 1981). Although state summaries report it to be common throughout Georgia (Golley, 1962; Laerm et al., 1981), specimen records are not evenly distributed in the state (Fig. 1a). Most specimen records are concentrated in both the northern and southern quarters of the state. Although the species presumably occurs in the central portion of Georgia, there are relatively few records to document its existence there. Eastern red bats are solitary and roost primarily in trees or shrubs. Roost sites usually are 1-7 m above ground and share common characteristics, such as lateral visual obscurity, absence of obstruction directly below, absence of lower perches, dark ground cover beneath the roost, sufficient adjacent vegetation to act as a wind screen, and location on the southern or southwestern side of the tree (Constantine, 1966).

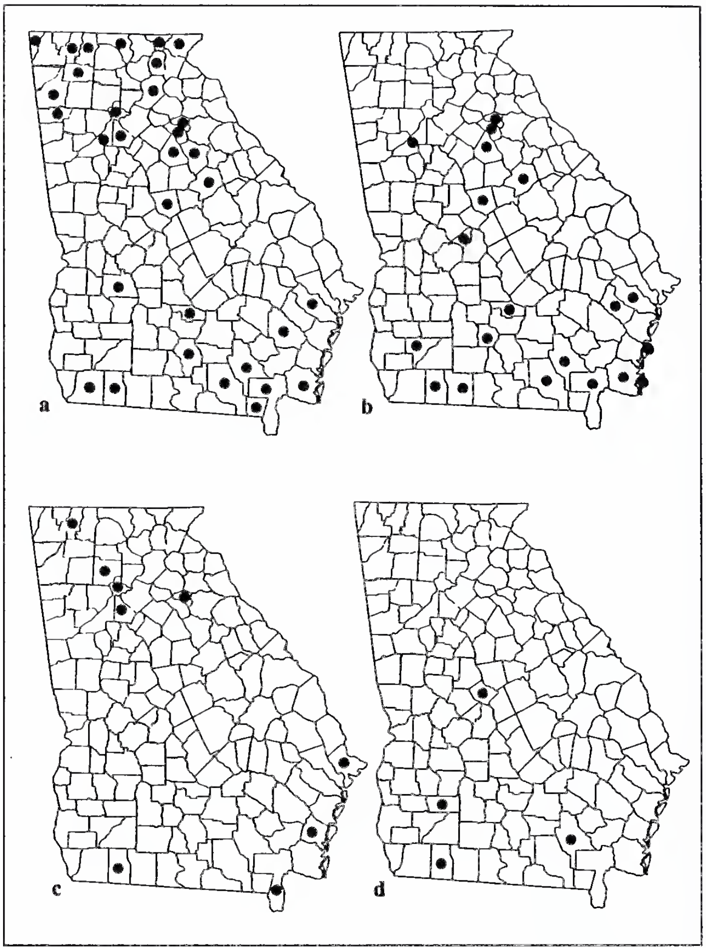

Fig. 1.—Distribution of the (a) eastern red bat *(Lasiurus borealis)*, (b) Seminole bat *(L. seminolus)*, (c) hoary bat *(L. cinereus)*, and (d) northern yellow bat *(L. intermedius)* in Georgia, based on specimen and literature records. Dots indicate counties in which records exist.

Other known locations of roosts include clumps of Spanish moss *(Tillandsia unsenoides;* Constantine, 1958), woodpecker cavities in trees (Fassler, 1975), and undersides of leaves of sunflowers *(Helianthus*—Downes, 1964). There are no estimates of population density for the species in Georgia.

Lasiurus seminolus.—Seminole bats are distributed primarily in the southeastern United States from eastern Texas and southern Oklahoma eastward to North Carolina (Hall, 1981). Although Barbour and Davis (1969) suggested that the range of this species coincided with the range of Spanish moss, Seminole bats regularly occur much farther north than the moss. Known distribution of Seminole bats in Georgia extends to the northernmost region of the Piedmont, but most records are concentrated in the southeastern corner of the state (Fig. 1b). Constantine (1958) found that Seminole bats in southwestern Georgia roosted in clumps of Spanish moss in both overcup oaks *(Q. lyrata)* and live oaks *(Q. virginiana).* In eastern Texas, *L. seminolus* is more common in pine forests than in oak-dominated forests (Schmidly et al., 1977), but there are no indications of habitat preferences for the species in Georgia. Laerm et al. (1980) observed Seminole bats feeding over a variety of forest and wetland habitat in Okefenokee Swamp. Population status of this species is unknown in Georgia.

Lasiurus cinereus.—Hoary bats occur throughout most of the United States (Hall, 1981). The species probably occurs throughout Georgia, but specimen records are rare in the state and are nonexistent in the central region (Fig. 1c). Hoary bats are solitary, tree-roosting species that tend to select roost trees near the edge of openings (Shump and Shump, 1982). Roosts are located on leaf-concealed branches 3-5 m above ground and with open space underneath (Constantine, 1958). Preferences for species of roost trees or forest type are unknown and the species forages above the canopy of most forest types (Black, 1974). Population estimates are not available, but it is regarded as locally common in Georgia.

Lasiurus intermedius.–Northern yellow bats are known from coastal plain habitats extending from southern Virginia to southern Texas in the United States (Hall, 1981). Barbour and Davis (1969) suggested that the distributional range of the northern yellow bat coincided with the range of Spanish moss. In Georgia, the species is restricted to the southern quarter of the state, where it was collected from only four counties (Fig. 1d). Northern yellow bats are solitary when roosting, but many individuals sometimes congregate in a single tree (Jennings, 1958), where they roost in clumps of Spanish moss or under dense outgrowths of leaves in live oaks. Little is known of the natural history of this species, and nothing is known about its population status (Kern, 1992). The northern yellow bat is listed as a species of concern by the Georgia Natural Heritage Inventory.

FOREST TRENDS IN GEORGIA

Timber-supply prospects are a continual concern for all components of forest industry (Cubbage et al., 1990). Forest-products firms want to insure that an adequate supply of wood fiber is available to furnish their processing facilities. Furthermore, supply and prices of wood are considered by industry when locating new mills, expanding existing mills, or maintaining existing plants. Landowners are interested in timber-supply trends because supply affects expected returns for all timber-growing investments. Forests also produce many outputs including human recreation and wildlife habitat. Demands for information concerning forest resources and timber supplies have culminated in forest-resource inventories and timber-supply projections for all states, regions, and the nation. Forest inventories have been performed in Georgia by the Southeastern Forest Experiment Station, United States Department of Agriculture Forest Service, periodically since 1936.

Thompson (1989) used data from the 1989 forest inventory to summarize present and future status of forest area and types, timber values, and timber growth in Georgia. In 1989, 65% of Georgia's land area was forested. The forested land area of Georgia declined slightly during the past 3 decades, dropping from 1.04 X 10^7 ha in 1961 to 9.7 X 10^6 ha in 1989. Pine cover types decreased steadily in area since 1953, dropping from 5.6 X 10^6 to 4.5 X 10^6 ha, and, although pine-plantation land area increased, there was a gradual decrease in natural pine-forest area. During the same time, area of hardwood land increased and volumes of hardwood nearly doubled. Based on the projection model developed by Cubbage et al. (1990), during the next 2 decades (1990-2010), all forest types, except natural stands of pine, will continue to increase slightly. Volumes of hardwoods are predicted to increase in the northern part of the state, but decease in southeastern Georgia.

DISCUSSION

Because roosting habits of lasiurine bats are known only from anecdotal accounts and there has been no comprehensive study of population density of these bats, it would be impossible to construct a model that would predict impact of any forest-management practice on the population of any lasiurine species. Much more detailed study of habitat-use patterns of each species of lasiurine is warranted. Reduction in size of radiotransmitters in recent years and development of ultrasonic detectors connected to activity recorders will greatly augment attempts to detail life history and population status of these species. Nevertheless, some inferences can be made about current and future status of lasiurine species in Georgia.

All lasiurines occasionally roost in clumps of Spanish moss when it is available. Projections of declines in volumes of hardwood in southeastern Georgia probably indicate that availability of Spanish moss also will decline in that area of the state. Losses of certain forest types in Florida may have contributed to a decline in abundance of *L. intermedius* (Kern, 1992). Abundances of Spanish moss already were reduced by a fungal disease (Kern, 1992), and by harvesting for packaging and florist use (Jennings, 1958; Lowery, 1974).

Projected increases in hardwood-forest volumes elsewhere in Georgia may indicate a stable future for at least the three species of lasiurines that occur in the northern two-thirds of the state. Increases in volumes of timber as forests mature and increases in mature hardwood forests undoubtedly bode well for all associated flora and fauna.

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DISTRIBUTION AND ABUNDANCE OF BATS IN CAVES AND MINES OF NORTHEASTERN MISSISSIPPI

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Little is known about Mississippi's bat fauna, which includes 14 species. The primary objective of this research was to survey caves and mines in northeastern Mississippi that could be inhabited by bats. Ten caves and one mine were located in Tishomingo (six caves and one mine) and Union (four caves) counties. Other than in Chalk Mine, Tishomingo Co., where bats were observed during every visit, and in Roberts Cave, Union Co., where one or two *Pipistrellus subflavus* were present only during winter months, no bats were observed in the caves. Chalk Mine serves as a day and night roost for *P. subflavus* throughout the year, and as a maternity site and hibernaculum. The greatest number of *P. subflavus* (12) were present in Chalk Mine during winter. *Eptesicus fuscus* and *Lasiurus borealis* were the only other species observed during the study.

Mississippi's bat fauna includes 14 species (E. R. Hall, 1981; Kennedy et al., 1974): little brown myotis *(Myotis lucifugus)*; Indiana myotis *(Myotis sodalis)*; southeastern myotis *(Myotis austroriparius)*; gray myotis *(Myotis grisescens)*; northern long-eared myotis *(Myotis septentrionalis)*; eastern pipistrelle *(Pipistrellus subflavus)*; big brown bat *(Eptesicus fuscus)*; yellow bat *(Lasiurus intermedius)*; red bat *(Lasiurus borealis)*; Seminole bat *(Lasiurus seminolus)*; hoary bat *(Lasiurus cinereus)*; evening bat *(Nycticeius humeralis)*; Rafinesque's big-eared bat *(Corynorhinus rafinesquii)*; Brazilian free-tailed bat *(Tadarida brasiliensis)*. Within Mississippi, the United States Fish and Wildlife Service lists two species of bats as endangered; *M. grisescens* and *M. sodalis.* Little is known about the biology of Mississippi's bat fauna (e.g., Crain and Cliburn, 1965; Kennedy et al., 1974; La Val, 1967). Most of the information regarding bats in the state has been gleaned from studies conducted in other states (e.g., Barbour and Davis, 1969; Crain and Packard, 1966; J. S. Hall, 1962; Humphrey, 1975; Humphrey et al., 1977; Jones, 1977; Jones and Suttkus, 1975; La Val, 1973; La Val and La Val, 1980; Lowery, 1974; Rice, 1955, 1957; Tuttle, 1976, 1979; Webster et al., 1980).

Caves and mines in northern Mississippi could harbor populations of many species of bats, including *M. grisescens* and *M. sodalis.* Objectives of this study were to survey caves and mines in northeastern Mississippi that may be occupied by bats, to determine abundance of these bats, and to provide management recommendations.

MATERIALS AND METHODS

We examined published maps (United States Geological Survey) and accounts in the literature (Cliburn and Middleton, 1983; Kennedy et al., 1974; Knight, 1972; Knight et al., 1974; La Val, 1967; Middleton, 1976; Woods and Wake, 1968), and interviewed conservation officers, other law-enforcement personnel, local residents, and landowners to determine locations of caves and mines in Alcorn, Benton, DeSoto, Lafayette, Lee, Marshall, Panola, Prentiss, Tate, Tawamba, Tippah, Tishomingo, Tunica, and Union counties, Mississippi. Mist nets were placed inside, across the entrance, or outside caves and mines, and over streams, ponds, and at the edge of Pickwick Lake to capture bats for identification. In caves where the bat fauna could accurately be determined without capturing bats, no mist nets were used. During surveys of Chalk Mine (6.4 km E Iuka, Tishomingo Co.) and caves, visual inspection of potential roosting places was made and a bat detector was used to locate bats when possible. An effort was made not to disturb hibernating bats of any species. Mingo Cave 1 (Tishomingo Co.), Mingo Cave 2 (Tishomingo Co.), Chalk Mine, and Roberts Cave (Union Co.) were examined at irregular intervals from March 1990 through March 1991 to determine if there was differential use of the sites by bats during the year.

RESULTS AND DISCUSSION

Ten caves and one mine were located in Tishomingo (six caves and one mine) and Union (four caves) counties

Table 1.—*Caves and mines in northeastern Mississippi.*

Name of cave/mine	County	Approximate location and comments
Chalk Mine	Tishomingo	Ca. 6.4 km E Iuka; also known as "abandoned silica mine" and Tripoli Cave; much evidence of disturbance by humans.
Mingo Cave No. 1	Tishomingo	At mile 308.4 on Natchez Trace Parkway; also known as Cave Spring; much visitation by humans.
Mingo Cave No. 2	Tishomingo	On Poole Farm south of Iuka; also known as Charles Poole Cave (Local residents indicated this is the only cave in the area, but Cliburn and Middleton, 1983, list specimens of *Plethodon glutinosus* from Mingo Cave No. 1, Mingo Cave No. 2, Charles Poole Cave, and Nunley Cave, indicating Mingo Cave No. 2 and Charles Poole Cave are not the same cave).
Charles Poole Cave	Tishomingo	Probably same as Mingo Cave No. 2 (see comments for Mingo Cave No. 2).
Nunley Cave	Tishomingo	A water-filled sinkhole southwest of Lucy's Cafe near Tishomingo.
Rock Creek Cave	Tishomingo	8 km SW Belmont; ca. 9 m deep and 1 m in diameter; wet walls.
Grubbs Wet Cave	Union	11.2 km SE New Albany; ca. 45 m long, 1-1.3 m in diameter; water-covered floor.
Grubbs Dry Cave	Union	11.2 km SE New Albany; ca. 24 m long, 3-5 m wide, and 1 m high; very dusty.
Roberts Cave	Union	6.4 km SE New Albany; ca. 24 m long, 1.3-1.7 m high; water in cave; open at both ends.
Land of Caves No. 1	Union	Not known by local persons (may refer to one of the entrances to Roberts Cave)
Land of Caves No. 2	Union	Not known by local persons (may refer to one of the entrances to Roberts Cave).

(Table 1). Other than in Chalk Mine, where bats were observed during every visit, and in Roberts Cave, where one or two *P. subflavus* were present only during winter months, no bats were observed in any other cave. Because of the presence of bats on a regular basis, and because previous research had documented the presence of *M. austroriparius, M. grisescens, M. septentrionalis, M. sodalis,* and *P. subflavus* at the site (Kennedy et al., 1974), Chalk Mine became the primary focus of research efforts.

An early description of Chalk Mine appears in Allison's (1907:13) paper on spring birds of Tishomingo Co., Mississippi. He states, "In a hillside rising immediately beyond a most precipitous descent, is the main opening to a 'silica' mine [so called by the natives] which was abandoned because of the fatality among laborers working up the material—though the miners themselves were not affected. The walls of the cave are of an amorphous, soft, chalky material, now damp and covered in many places with slime and moss."

Referring to the geologic formation associated with Chalk Mine, Merrill et al. (1988) recounted the geology and history of the mine. The upper portions of the Fort Payne Formation have weathered to a pulverulent, siliceous phase generally referred to as tripoli or silicastone. These deposits occur locally in a belt extending from northeastern Wayne Co., Tennessee, southward into northwestern Alabama and northeastern Mississippi. Tripoli was mined by hand, loaded onto tram cars and hauled on a tram down the valley. The main entrance has collapsed, and entry is achieved through a small air vent into the main shaft area.

We observed graffiti painted on the walls inside and at the entrance of Chalk Mine, trash inside and outside the mine, smoke from fires inside and outside the mine, and we saw several persons entering and leaving the mine. However, during non-summer months, there appears to be little visitation by humans. Most people approach the site by boat on Pickwick Lake, then walk ca. 300 m to the entrance of the mine.

In addition to Chalk Mine, *M. austroriparius* has been reported from several counties in Mississippi (Kennedy et al., 1974; La Val, 1967, 1970; Wolfe, 1971). The last records of occurrence of this species at Chalk Mine were in the late 1930s (La Val, 1967). We did not encounter this species.

Myotis grisescens is known only from Chalk Mine in Mississippi (Kennedy et al., 1974; La Val, 1967; White, 1961; Wolfe, 1971). We did not encounter this species, but colonies of this species are present near the Tennessee River in nearby Alabama (La Val, 1967).

White (1961) was the first to document the presence of *M. septentrionalis (=M. keeni)* in Mississippi. Apparently, all records of this species are associated with Chalk Mine (Kennedy et al., 1974). Prior to La Val's visit to Chalk Mine on 5 August 1966, collection dates for all specimens were in the late 1930s (La Val, 1967). In 1966, R. K. La Val observed one *M. septentrionalis* and one *P. subflavus* inside Chalk Mine; the mine already was heavily disturbed by activity of humans (R. K. La Val, in litt.). A report on mammals of Shiloh National Military Park, Tennessee, verifies the recent occurrence of *M. septentrionalis* within ca. 80 km of Mississippi (M. L. Kennedy, in litt.). In addition, there is a record of this species from near Red Bay, Franklin Co., Alabama, during 1990 (Hilton, 1993; Hilton and Best, 2000). Thus, a small population of *M. septentrionalis* persists in the vicinity of northeastern Mississippi.

The only records of *M. sodalis* for Mississippi are from the late 1930s. Five specimens were collected from Chalk Mine on 16 July 1939, and 11 were collected from the Tennessee River Area on 10 August 1937 (La Val, 1967). We did not encounter this species.

Previous accounts have listed specimens of *P. subflavus* from Chalk Mine (Davis, 1959; Kennedy et al., 1974; White, 1961), and we found this species in Chalk Mine during each of our visits (Table 2). Chalk Mine serves as a day and night roost for *P. subflavus* throughout the year. In addition, it serves as a maternity site and as a hibernaculum. Observations during winter provided the greatest number of individuals (12); some were covered with condensed water indicating they may have been in hibernation. That they were not in hibernation for long periods of time was indicated by their movement between times of observation. Individuals were hanging from the walls and ceiling at heights of 2-5 m. Based upon observations of several hundred individuals in similarly sized (or smaller) caves in Alabama during winter months (Best et al., 1993), frequent entry by humans may reduce the number of bats using Chalk Mine as a hibernaculum.

A male *E. fuscus* was captured in a mist net set inside Chalk Mine on 17 August 1990. One or two individuals were observed in the mine during December, January, and February (Table 2). Observations in

Table 2.—*Numbers and species of bats occurring inside Chalk Mine, 6.4 km E Iuka, Tishomingo Co., Mississippi, 1990-1991.*

	Numbers and species of bats observed	
Date	*Eptesicus fuscus*	*Pipistrellus subflavus*
10 March	0	1
9 June	0	6
27 June	0	5 (+2 young)
15 July	0	3 (+3 young)
17 August	1	5
28 October	0	10
1 December	0	12
28 December	2	12
26 January	1	12
15 February	1	8
8 March	0	6

winter did not indicate the animals were in hibernation, although none flew from roost sites. Big brown bats observed in winter were within the twilight area near the entrance. This species had not been reported previously from Chalk Mine.

The only other species of bat we encountered near Chalk Mine was *L. borealis.* This species frequently was captured in mist nets placed in the wooded area near Chalk Mine (it was especially common to capture this species in nets placed just upstream from the nearby arm of Pickwick Lake ca. 200 m from the mine), but none occurred in the mine. M. L. Kennedy captured one *L. borealis* in a mist net placed outside of Chalk Mine on 3 January 1977 (M. L. Kennedy, in litt.).

In the past, Chalk Mine has been an important site for bats. Although there are no indications that the mine ever served as home for large colonies, most records for the rarest species of bats in Mississippi have come from the mine. The authors have recommended that the mine be purchased by the state of Mississippi and that the entrance is fenced or gated to keep humans out of the mine. Perhaps, this mine will again become a home for rare species of bats.

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BODY SIZE, REPRODUCTIVE BIOLOGY, AND SEX RATIO OF A YEAR-ROUND COLONY OF *EPTESICUS FUSCUS FUSCUS* AND *TADARIDA BRASILIENSIS CYNOCEPHALA* IN EASTERN ALABAMA

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We studied variation in body size, reproductive biology, and sex ratio of a year-round colony of *Eptesicus f. fuscus* and *Tadarida brasiliensis cynocephala* located on the campus of Auburn University, Lee Co., Alabama. Females of *E. f. fuscus* had greater mass and length of body than males, there were no differences between genders of *T. b. cynocephala* in mass, but males were larger than females in length of body. Length of testis was greatest in October and least in February for *E. f. fuscus,* and greatest during February and least in June for *T. b. cynocephala.* All females of *E. f. fuscus* examined in May had embryos in both uterine horns; parturition took place in late May-early June. Pregnant *T. b. cynocephala* had embryos only in the right uterine horn; parturition occurred in late May-early June. The number of females in the population of *E. f. fuscus* usually was greater than the number of males; males of *T. b. cynocephala* out-numbered females most of the year. When compared to single-species colonies, there were only slight differences in this mixed colony, which may be attributable to geographic variation in climatic conditions.

Roosts are critical sites that are required for survival of many species of vertebrates, e.g., roost sites may be used for breeding, rearing young, and protection against weather and predators. For bats, roost sites are especially important. Most species spend >50% of their life at one type of roost or another; thus, roosts have influenced behavior and evolution of bats (Kunz, 1982).

Generally, bats form single-species aggregations within a roosting area, but mixed-species use of roosting sites has been observed in many species (e.g., Barbour and Davis, 1969; Eads et al., 1957; Hermanson and Wilkins, 1986; Jennings, 1958; Lowery, 1974; Phillips, 1966; Sherman, 1937). Most mixed-species associations result from bats having similar diurnal requirements and a lack of suitable roost sites (Bradbury, 1977). Graham (1988) investigated use of diurnal roosts by several species of bats and found that some species were more generalized in their requirements and were more likely to share roost sites with other species of bats. Roost sharing may involve costs and benefits. Costs may include increased incidence of disease and parasites, competition for resources, opportunity for detection by predators, and mortality of infants. Benefits may include increased detection of predators and reduced costs of thermoregulation (Bradbury, 1977; Graham, 1988; Kunz, 1982). Nevertheless, most interspecific associations in roosts probably are neutral (Bradbury, 1977; Graham, 1988; Swift and Racey, 1983).

A roost used by both *Eptesicus fuscus fuscus* and *Tadarida brasiliensis cynocephala* was located in the attic of Samford Hall on the campus of Auburn University, Lee Co., Alabama; both of these species had inhabited brick buildings on campus for >50 years (Barkalow, 1939). In 1990, the attic of Samford Hall contained ca. 700 bats of each species, but because of renovation of the structure the colony was destroyed in 1994. Although single-species aggregations of bats were present in the colony, many clusters of bats contained both species in direct contact. Close physical association between *E. f. fuscus* and *T. b. cynocephala* may have been facilitated by partitioning of resources between these taxa. For example, *E. fuscus* primarily feeds upon Coleoptera (Kurta and Baker, 1990; Phillips, 1966), whereas Lepidoptera make up ca. 90% of the diet of *T. brasiliensis* (Ross, 1961; Storer, 1926; Wilkins, 1989). Because differences in diet probably reduce competition for food resources in the area surrounding the roost, this may be a significant factor in allowing these bats to inhabit the same roost site. However, it is unknown whether species inhabiting such mixed-species colonies differ morphologically, reproductively, or behaviorally from other populations of the species that do not share roost sites.

The purposes of our study were to examine patterns of variation in body size between genders, among months, and between species, in reproductive characters among months for each species, and in sex ratio of the population among months for *E. f. fuscus* and *T. b. cynocephala* inhabiting the same roost. Because gestation and lactation are among the most energy demanding periods for females (Kunz, 1974b; Pistole, 1989), we also wanted to document whether temporal adjustments in reproductive activity may have occurred in response to these bats roosting together.

MATERIALS AND METHODS

Samford Hall, located on the campus of Auburn University, Lee Co., Alabama, is a four-story structure with a double-roofed design in the attic, which provided year-round shelter for bats. *E. f. fuscus* and *T. b. cynocephala* were sampled monthly from February through November 1990. A total of 229 bats (31 males, 65 females of *E. f. fuscus*; 74 males, 59 females of *T. b. cynocephala*) was examined to determine body size, reproductive condition, and incidence of parasitism (Durden et al., 1992; Hilton, 1993; Hilton and Best, 2000). Bats were collected by hand, sacrificed with chloroform, and measurements of mass and length of body were taken to the nearest 0.5 g and 1 mm, respectively. Position of embryo in the uterus, number of embryos, length of testis, and sex ratios also were recorded. Specimens were deposited in the Auburn University Museum.

Character heterogeneity (between species, between genders, and among months) was tested with a one-way analysis of variance, and, when statistically significant variation was present ($P \le 0.05$), a Student-Neuman-Kuels (SNK) a posteriori test for multiple comparisons among means was used to determine maximally nonsignificant subsets. All statistical analyses were conducted using SPSS/PC+ (Norŭsis, 1990).

RESULTS AND DISCUSSION

Mass.—Burnett (1983) reported that females of *E. fuscus* were slightly larger than males. In Alabama, average mass of nonpregnant females of *E. f. fuscus* (17.1 g) also was greater than that of males (13.6 g; $P < 0.001$; *d.f.* = 1,86; F-ratio = 29.4); minimum mass for both genders was attained in April (11.0 and 12.3 g for males and females, respectively; Fig. 1a). This pattern is similar to that reported for females of *E. f. fuscus* in Kansas (Kunz, 1974a). In our study, average mass of males of *E. f. fuscus* decreased from February to April, fluctuated slightly in summer, then increased until maximum mass was reached in November (Fig. 1a), but no statistically significant difference was detected among months by SNK analysis ($P = 0.03$; Table 1). Average mass of females of *E. f. fuscus* declined from February to April; gestation caused mass to increase from its minimum in April (12.3 g) to its maximum in May (20.6 g). After parturition, mass decreased in June, increased from July to September, when average mass almost equaled that during pregnancy, then declined through November (Fig. 1a). When pregnant females were excluded from analyses, there also was significant variation among months ($P < 0.001$);

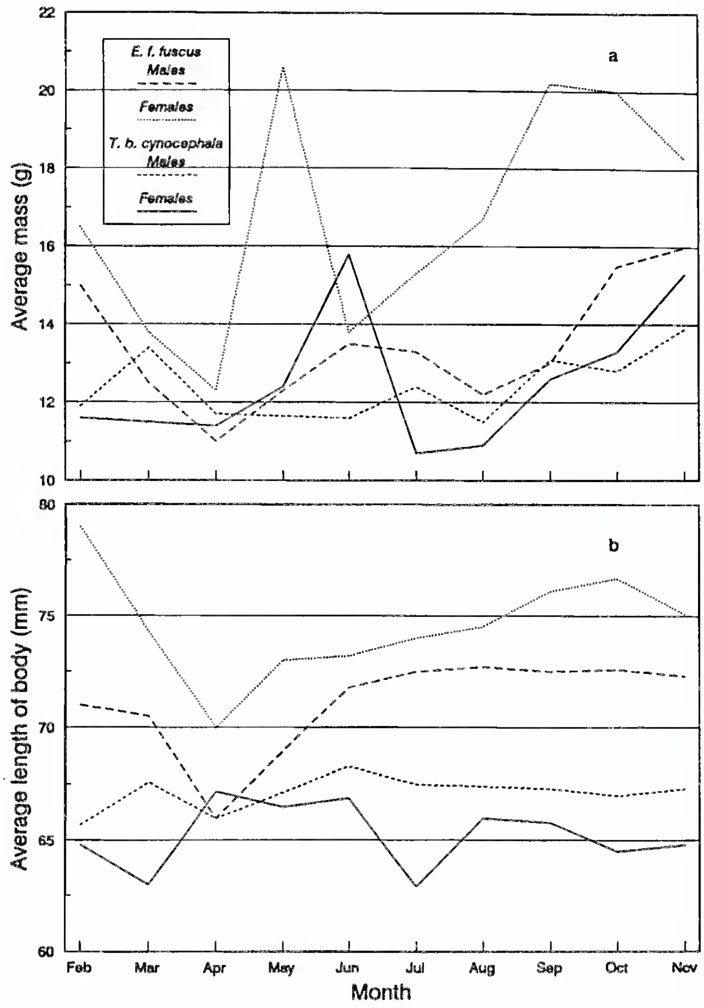

Fig. 1.—Variation in a) average body mass and b) length of body of all males and all females of *Eptesicus f. fuscus* and *Tadarida brasiliensis cynocephala* at Auburn University, Lee Co., Alabama, in 1990.

Table 1.—*Results of one-way analysis of variance of morphologic variation for two species of bats occupying the same roost in eastern Alabama. Minimally significant variation among months is assumed where* P < *0.05 (*). Means and results of Student-Neuman-Kuels a posteriori tests for multiple comparisons among means are given for each comparison.*

Character	Sex	*d.f.*	*F*-ratio	Results of Student-Neuman-Kuels analysis									
Eptesicus f. fuscus													
Mass	Male	9,21	2.7*	Apr	Aug	May	Mar	Sep	Jul	Jun	Feb	Oct	Nov
				11.0	12.2	12.3	12.5	13.0	13.3	13.5	15.0	15.5	16.0
	Female	8,48	8.8*	Apr	Jun	Mar	Jul	Feb	Aug	Nov	Oct	Sep	
				12.3	13.8	13.8	15.3	16.5	16.7	18.3	20.0	20.2	
Length of body	Male	9,21	1.3ns	Apr	May	Mar	Feb	Jun	Nov	Jul	Sep	Oct	Aug
				66.0	69.0	70.5	71.0	71.8	72.3	72.5	72.5	72.6	72.7
	Female	8,49	1.5ns	Apr	Jun	Jul	Mar	Aug	Nov	Sep	Oct	Feb	
				70.0	73.2	74.0	74.3	74.5	75.1	76.1	76.7	79.0	
Length of testis	Male	9,17	4.7*	Feb	Apr	Jun	Mar	May	Jul	Sep	Nov	Aug	Oct
				4.0	5.0	5.0	5.5	6.0	6.0	7.0	7.5	7.7	9.0
Tadarida brasiliensis cynocephala													
Mass	Male	8,64	6.8*	Aug	Jun	Apr	Feb	Jul	Oct	Sep	Mar	Nov	
				11.5	11.6	11.7	11.9	12.4	12.8	13.1	13.4	13.9	
	Female	7,31	8.5*	Jul	Aug	Apr	Mar	Feb	Sep	Oct	Nov		
				10.7	10.9	11.4	11.5	11.6	12.6	13.3	15.3		
Length of body	Male	8,65	0.9ns	Feb	Apr	Oct	Nov	Sep	Aug	Jul	Mar	Jun	
				65.7	66.0	67.0	67.3	67.3	67.4	67.5	67.6	68.3	
	Female	7,31	2.4*	Jul	Mar	Oct	Nov	Feb	Sep	Aug	Apr		
				62.9	63.0	64.5	64.8	64.8	65.8	66.0	67.2		
Length of testis	Male	8,56	3.4*	Jun	Jul	Aug	Sep	Nov	Oct	Apr	Mar	Feb	
				3.3	4.0	4.5	5.0	5.0	5.1	5.3	5.6	5.7	

mass of females in April was significantly less than that in August through November, and mass in October and September was greater than that in all other months (Table 1). Pistole (1989) reported that females of *E. fuscus* deposit fat, in anticipation of hibernation, 1 month earlier than do males. This also was shown by the population in Alabama; females had a noticeable increase in mass from August to September, then males showed a similar acceleration from September to October (Fig. 1a).

La Val (1973) and Lowery (1974) reported that average mass of females of *T. b. cynocephala* often was more than that of males in Louisiana, but we found no significant difference in mass between genders in Alabama (average mass: males, 12.5 g, females, 12.1 g; $P = 0.13$; *d.f.* = 1,110; *F*-ratio = 2.4). For males, mass fluctuated from February through October, then increased to the maximum in November (Fig. 1a). Mass of males was significantly greater in March, September, and November than in February, April, June, and August ($P < 0.001$; Table 1), indicating a tendency to add mass following hibernation and before entering hibernation. In February, females of *T. b. cynocephala* had an average mass of 11.6 g. Mass stayed near this level until June when it increased to a maximum of 15.8 g during gestation (Fig. 1a), mass was least in July and August, and then a steady increase occurred from August to November, when mass almost equaled that during pregnancy. Mass of nonpregnant females was significantly greater in November than in any other month, and mass in October was significantly greater than in July and August ($P < 0.001$; Table 1), indicating a pre-hibernation gain in mass. A similar pre-hibernation increase in mass was noted for this taxon in Louisiana (La Val, 1973).

Length of body.—Phillips (1966) and Burnett (1983) reported that males of *E. fuscus* were smaller than females. Likewise, in our study of *E. f. fuscus,* average length of body of males (71.2 mm) was significantly smaller than that of nonpregnant females (74.9 mm; $P < 0.001$; *d.f.* = 1,87; *F*-ratio = 20.0). Average length of body for males ranged from 66.0 mm in April to 72.7 mm in August, but there was no significant difference among months ($P = 0.28$; Fig. 1b; Table 1). Average length of body in females of *E. f. fuscus* was greatest in February and least in April, and there also was no significant difference among months ($P = 0.18$; Fig. 1b; Table 1).

For *T. b. cynocephala,* average length of body of males was larger than females in all months, except April (Fig. 1b); males (66.8 mm) were significantly larger than females for this character (64.9 mm; $P < 0.001$; *d.f.* = 1,111; *F*-ratio = 14.1). For males, length of body was least in February and greatest in June, but there were no significant differences among months ($P = 0.51$; Fig. 1b; Table 1). Average length of body for nonpregnant females was greatest in April and least in July, and measurements for these two months were significant different from each other ($P = 0.05$; Table 1), possibly indicating differences in size of body before and after pregnancy, respectively.

Length of testis.—*Eptesicus fuscus* copulates in autumn (Phillips, 1966). Length of testis of *E. f. fuscus* was least in February, generally increased throughout the year to a maximum in October, then decreased in November (Fig. 2; Table 1). There were significant differences among months ($P = 0.003$; Table 1), and length of testis in February, April, and June was smaller than in August, October, and November. Phillips (1966) also found similar changes in length of testis in Kansas, but maximum size of testes was reached in August. Apparently, *E. f. fuscus* in Alabama breed later in the year than in Kansas, but this probably is related to geographic variation in climate and not the result of sharing a roost with *T. b. cynocephala.*

Length of testis of *T. b. cynocephala* was greatest in February and declined to a minimum in June, increased in September, and varied only 0.1 mm through November (Fig. 2). There were significant differences among months ($P < 0.01$); length of testis in June was significantly smaller than in March and February (Table 1). Previous studies of this subspecies in Florida (Sherman,

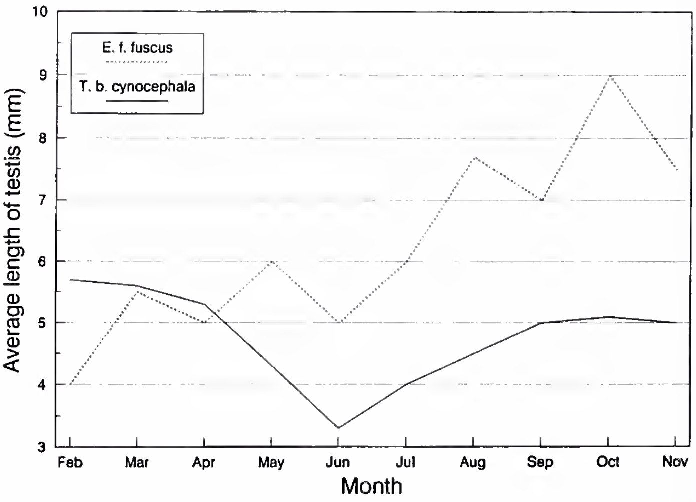

Fig. 2.—Variation in average length of testis of *Eptesicus f. fuscus* and *Tadarida brasiliensis cynocephala* at Auburn University, Lee Co., Alabama, in 1990.

1937) and Louisiana (Pagels and Jones, 1974) revealed that copulation occurs in March. Based upon our measurements of length of testis, breeding occurs in eastern Alabama in February or March.

Number of embryos.—Average number of offspring per year for *E. fuscus* in eastern North America is two (Barbour and Davis, 1969; Christian, 1956; Kunz, 1974a). In Alabama, all pregnant *E. f. fuscus* had embryos in both uterine horns in May. The average crown-rump length of embryos was 21.0 mm ($n = 7$); no embryos were found in other months. With embryos this large in May, the *E. f. fuscus* we studied in Alabama must have been pregnant in April. Generally, *E. f. fuscus* from the southern part of its range are pregnant in April and parturition occurs in May (Cockrum, 1955). The first lactating *E. f. fuscus* that we observed with a young-of-the-year was on 6 June, along with many pregnant females, and this young-of-the-year weighed 8.5 g. Due to large mass of the young bat and because mass of females decreased from May to June, we assumed that parturition began in late May. Our findings regarding time of gestation and parturition coincide with previous reports (Barbour and Davis, 1969; Brimley, 1923; Gates, 1937; Harper, 1929; Kunz, 1974a).

Females of *T. b. cynocephala* give birth to one precocial young each year (Sherman, 1937). Similar to previous reports on this taxon (Sherman, 1937; Wilkins, 1989), all pregnant *T. b. cynocephala* that we examined in Alabama had embryos only in the right uterine horn; embryos were present in April (average = 6.0 mm in crown-rump length, $n = 1$), May (average = 18.0 mm, $n = 12$), and June (average = 31.0 mm, $n = 8$). Average crown-rump length of embryos that we observed in June (31.0 mm) was greater than lengths (25-30 mm) reported previously (Barbour and Davis, 1969; Pagels and Jones, 1974; Sherman, 1937; Wilkins, 1989). Sherman (1937) and La Val (1973) found that parturition in populations of *T. b. cynocephala* in Florida and Louisiana, respectively, usually took place in early June. In Louisiana, Pagels and Jones (1974) observed vaginal plugs and La Val (1973) found embryos in this taxon as early as March; these observations support Sherman's (1937) conclusion that the gestation period is 11-12 weeks. In our study, mass of females of *T. b. cynocephala* decreased sharply from June to July, indicating this was when parturition occurred in eastern Alabama (Fig. 1a). No evidence of twins or triplets, which previously have been reported for *T. b. cynocephala* in Alabama (Di Salvo et al., 1969), was observed.

Sex ratio.—Females represented ≥50% of the population of *E. f. fuscus* every month, but males always were present. Greatest percentages of females (83.3%) were in July and September. The sex ratio we observed in Alabama differs substantially from sex ratios observed in maternity colonies in Kentucky; only a few males were present in those colonies in late May and early June. From late June through August, number of males increased, approaching the same frequency as females in the populations (Barbour and Davis, 1969; Davis et al., 1968). Differences between colonies in Kentucky and the one we studied in Alabama may be related to geographic variation in climatic and habitat variables, or more likely, to our colony serving as both a hibernaculum and maternity colony. Males never composed the majority of the population, but they always were present in frequencies of 16.7-50.0% of the population. In Kansas (Phillips, 1966), Minnesota (Goehring, 1972; Rysgaard, 1942), Pennsylvania (Mohr, 1942, 1945), and Canada (Hitchcock, 1965), males of *E. fuscus* often were more numerous than females in hibernacula, but during winter months in eastern Alabama, there were more females in the colony.

Percentage of females in the population of *T. b. cynocephala* (Fig. 3) was lowest in March (8.3%) and greatest in May (100%). Sherman (1937) reported similar observations in Florida. In our study, males of *T. b. cynocephala* composed the majority of the population in February, March, August, September, and November, the genders were equally represented in April and October,

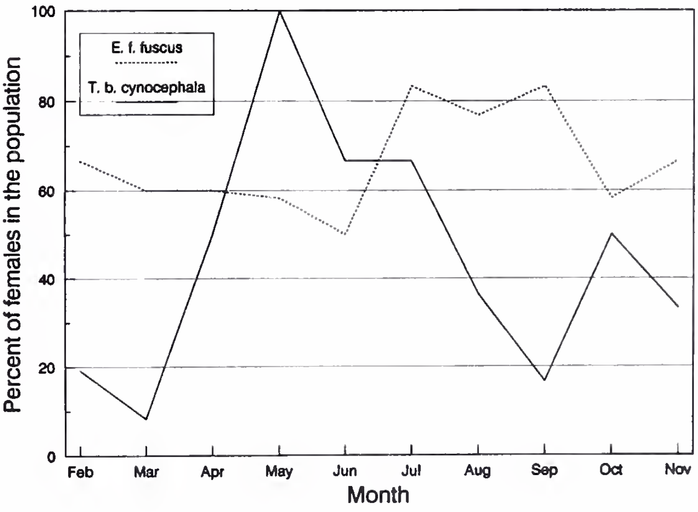

Fig. 3.—Variation in percentage of females in the population of *Eptesicus f. fuscus* and *Tadarida brasiliensis cynocephala* at Auburn University, Lee Co., Alabama, in 1990.

and females outnumbered males in May, June, and July (Fig. 3). Our observation of a sex ratio of 0.50:1.00 in July differs from the ratio of 1.00:0.81 reported for males and females in July in Louisiana (Pagels and Jones, 1974), and our observations of males being more frequent in the population during several months differs from the dominance of females in all samples examined in Louisiana by La Val (1973). At our study site, percentage of females was greatest in May (100%), indicating that males were roosting at other sites at this time.

Interspecific comparisons.—Average mass (13.6 g), length of body (71.2 mm), and length of testis (6.5 mm) of males of *E. f. fuscus* were significantly greater than in *T. b. cynocephala,* which averaged 12.5 g ($P = 0.001$; *d.f.* = 1,102; *F*-ratio = 11.2), 66.8 mm ($P < 0.001$; *d.f.* = 1,103; *F*-ratio = 54.2), and 5.1 mm ($P < 0.001$; *d.f.* = 1,90; *F*-ratio = 20.8), respectively. Average mass (17.1 g) and length of body (74.8 mm) of nonpregnant females of *E. f. fuscus* were significantly greater than in *T. b. cynocephala,* which averaged 12.1 g ($P < 0.001$; *d.f.* = 1,94; *F*-ratio = 79.4) and 64.9 mm ($P < 0.001$; *d.f.* = 1,95; *F*-ratio = 203.4), respectively.

Percentage of females in the colony varied between species (Fig. 3). Average percentage of females (66.4%; range = 50.0-83.3) in the population of *E. f. fuscus* was significantly larger than the average (44.7%; range = 8.3-100) for *T. b. brasiliensis* ($P = 0.04$; *d.f.* = 1,18; *F*-ratio = 5.1).

Parturition occurred slightly earlier in *E. f. fuscus* than in *T. b. cynocephala,* but both species had their young in late May-early June. *E. f. fuscus* had two young and *T. b. cynocephala* had one young.

While quantifying incidence of ectoparasites within our study population, Durden et al. (1992) observed that most mites recovered from *E. fuscus* were *Chiroptonyssus robustipes,* a mite that typically lives in association with *T. brasiliensis.* In contrast, only two specimens of *Steatonyssus occidentalis,* a specific ectoparasite of *E. fuscus,* were recovered from *T. brasiliensis.* Thus, from the perspective of cross-infestations of ectoparasites, *E. fuscus* appears to be at greater risk from sharing roosts with *T. brasiliensis* (Durden et al., 1992). Conversely, Hilton (1993) and Hilton and Best (1999) found endoparasites of the two species to differ significantly; trematodes predominated in *E. fuscus* and nematodes in *T. brasiliensis.*

Although we found many similarities between our results and those of other studies, we also found some differences in variation in body size and reproductive biology. Because these differences may be due to geographic or annual variation in climatic or other habitat variables, it was not possible to ascertain any patterns that indicated interspecific interactions were responsible for the observed differences. Because these bats differ in diet, parasites, body size, reproductive biology, and sex ratio, their effects upon each other at this common roost site appear insignificant.

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GASTROINTESTINAL HELMINTH PARASITES OF BATS IN ALABAMA

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Gastrointestinal tracts of 324 bats representing 10 species from 27 locations in Alabama were examined. Helminth parasites occurred in 121 (37.3%) of the bats; 14 (4.3%) had cestodes, 47 (14.5%) had nematodes, and 77 (23.8%) had trematodes. Fifteen bats (4.6%) were parasitized by two types of helminths, and one had all three types of helminths. There was no significant difference between numbers of big brown bats *(Eptesicus fuscus)* and Brazilian free-tailed bats *(Tadarida brasiliensis)* that were parasitized, but *E. fuscus* was more likely to have trematodes and *T. brasiliensis* was more likely to have nematodes. Prevalences of parasites (percentage of infected hosts) were: *E. fuscus,* 26.6% ($n = 128$); red bat *(Lasiurus borealis),* 80.0% ($n = 10$); evening bat *(Nycticeius humeralis),* 40.0% ($n = 15$); southeastern myotis *(Myotis austroriparius),* 72.7% ($n = 11$); eastern pipistrelle *(Pipistrellus subflavus),* 71.1% ($n = 45$); *T. brasiliensis,* 25.7% ($n = 109$).

Bats are hosts to many internal parasites (Stiles and Nolan, 1931; Webster, 1973). Ubelaker's (1970) review of endoparasites of bats included one genus of acanthocephalan, 10 genera of cestodes, 24 genera of nematodes, 13 genera of protozoans, and 42 genera of trematodes. Endoparasites have been recorded from carnivorous (Peterson and Kirmse, 1969), frugivorous (Bray, 1984; Ubelaker et al., 1977), insectivorous (Duszynski et al., 1988), piscivorous (Fischthal and Martin, 1978; Zdzitowiecki and Rutkowska, 1980), and sanguivorous (Greenhall and Schmidt, 1988) bats. Despite the long scientific history documenting parasites in bats from throughout the world (Webster, 1973), endoparasites of bats in North America are poorly known (Coggins, 1988). There are only five published reports on internal parasites of bats from the southeastern United States; three are on helminth parasites of bats from Louisiana, Mississippi, Tennessee (Byrd and Macy, 1942), Texas, Louisiana (Martin, 1976), and Florida (Loftin, 1961), and two are on protozoan parasites of bats from Alabama (Wheat, 1975) and Florida (Foster, 1979).

There have been three parasitologic studies of bats in Alabama. White (1959) reported 30 species of acarine mites from 10 species of bats. Wheat (1975) described *Eimeria macyi* (Protozoa: Eimeriidae) from a *P. subflavus* that was collected in Lion's Den Cave, Clarke Co. More recently, Durden et al. (1992) recorded seven species of acarine mites on cohabitating *E. fuscus* and *T. brasiliensis* from Auburn University, Lee Co. None of these studies have involved helminth parasites of bats. Because limited emphasis has been placed on helminthiases of bats in any geographic area (Nickel and Hansen, 1967), we conducted this study to identify species of bats in Alabama that have a parasitic helminthofauna. Additional goals of this study were to examine variations in helminth faunas with respect to species of host, collection locality, sex of host, season, and interrelationships of parasitic helminths.

MATERIALS AND METHODS

A total of 324 specimens representing 10 of the 16 species of bats that occur in Alabama (Best et al., 1993; E. R. Hall, 1981) was examined from 27 locations during this study (Appendix I). Of these specimens, 88 were *E. fuscus* and 105 were *T. brasiliensis* taken from the attic of Samford Hall, Auburn University. Samford Hall is a large, four-story building with a double-roofed design that serves as a year-round residence for both species of bats (Durden et al., 1992; Henry et al., 2000). During each month from February through November 1990, ≤12 *E. fuscus* and *T. brasiliensis* were either collected from their roost sites by hand or trapped with a harp trap. Care was taken not to collect young-of-the-year or females that were caring for young. Other species of bats were collected February 1990-April 1992. Collection methods included mist nets placed over bodies of water, capturing bats in residences, and removal of bats from roosts in caves. Several bats were brought to our laboratory by persons who found the bats in their homes.

Individual bats were placed into 250-ml beakers. Each beaker was sealed with a perforated cardboard top, and placed in a refrigerator (4.4°C) for 6-12 h to allow for passage of ingesta that otherwise may have impeded dissection. Bats were euthanized with chloroform and brushed with a toothbrush to collect external parasites for another study (Durden et al., 1992). The gastrointestinal tract (stomach, small and large intestines, and rectum) of each bat was removed, preserved in 10% formalin, and later inspected for parasites with the aid of a dissecting microscope. Parasites discovered in gastrointestinal tracts were removed using a camel-hair brush or dissecting needle and placed into 70% ethanol for storage. Voucher specimens of bats were prepared and deposited in the Auburn University Museum.

One cestode from each infected bat (n = 14) and one trematode were examined using scanning electron microscopy. Specimens were dehydrated by placing them into microporous specimen capsules (Electron Microscopy Sciences, Fort Washington, PA), which were placed into vials of 70, 80, 90, and 100% ethanol; 15 min for each change. The final change of ethanol was repeated twice. Alcohol was then removed from dehydrated specimens using a DCP-1 Critical-Point Drying Apparatus (Denton Vacuum, Inc., Cherry Hill, NJ), or by treatment with hexamethydisilazane (HMDS). Specimens were prepared with HMDS as follows: 100% ethanol was removed from the vial, HMDS was added, and immediately removed; fresh HMDS was added and allowed to remain for 15 min, the HMDS was removed, and fresh HMDS was added for another 15 min; specimens were then placed onto filter paper in a fume hood to allow for evaporation of the HMDS; fully dried specimens were affixed to carbon tape on aluminum stubs and sputter coated with gold-palladium for 30-50 s. Examination was conducted with a Zeiss DSM 940 digital scanning electron microscope.

Model I contingency table analyses using the G-test of independence were conducted on frequencies of parasitism with respect to taxon of parasite, and species, sex, and collection locality of host. G-test for goodness of fit was used to determine presence or absence of interrelationships in occurrence of parasite taxa (Sokal and Rohlf, 1981).

RESULTS AND DISCUSSION

Of the 324 bats examined, 121 (37.3%) had helminth parasites. Cestodes were found in 14 (4.3%) bats, 47 (14.5%) had nematodes, and 77 (23.8%) had trematodes. Frequency of parasitism and prevalence of parasites for each species of bat are summarized in Table 1. When we compared our results with other surveys of multiple species of bats (Blankespoor and Ulmer, 1970; Nickel and Hansen, 1967; Pistole, 1988), we observed that overall prevalence varied among studies, and that trematodes were the most prevalent helminths, nematodes were next, and cestodes were least prevalent. For example, Nickel and Hansen (1967) surveyed eight species of bats (n = 65) from seven counties in Kansas, Nebraska, and Oklahoma, and found that overall prevalence of parasites was 38.5%. When individual taxa were considered, trematodes (26.2%) were most prevalent, followed by nematodes (24.6%) and cestodes (7.7%). Similar results were seen in a study of

Table 1.—*Frequencies (F) and prevalences in percent (P) of three taxa of gastrointestinal-helminth parasites in 10 species of bats in Alabama.*

		Cestoidea		Nematoda		Trematoda	
Species	*n*	F	P	F	P	F	P
Eptesicus fuscus	128	0	—	5	3.9	31	24.2
Lasiurus borealis	10	3	30.0	4	40.0	4	40.0
Lasiurus cinereus	1	1	100	1	100	0	—
Lasiurus seminolus	3	3	100	0	—	3	100
Myotis austroriparius	11	2	18.2	2	18.2	6	54.5
Myotis septentrionalis	1	0	—	0	—	1	100
Nycticeius humeralis	15	3	20.0	6	40.0	1	6.7
Pipistrellus subflavus	45	1	2.2	3	6.7	29	64.4
Corynorhinus rafinesquii	1	0	—	0	—	0	—
Tadarida brasiliensis	109	1	0.9	26	23.8	2	1.8

64 bats, representing six species from 16 localities in Iowa (Blankespoor and Ulmer, 1970), and in a more recent study of 888 bats, representing nine species, from 65 counties in Indiana (Pistole, 1988).

Only 16 (4.9%) of the parasitized bats in our study had representatives of more than one phylum or class of helminths; three (<1%) were parasitized by nematodes and trematodes, seven (2.2%) by cestodes and trematodes, five (1.5%) by cestodes and nematodes, and one by cestodes, nematodes, and trematodes (Table 2). Analyses of these data using the *G*-test for goodness of fit showed that bats were most likely to have only cestodes, nematodes, or trematodes, and not a combination of nematode-trematode ($G = 82.89 \gg X^2_{0.05[2]}$), cestode-trematode

Table 2.—*Frequencies of Cestoidea (C), Nematoda (N), and Trematoda (T) in bats from Samford Hall, bats from elsewhere in Alabama, and for the two species of bats found in Samford Hall and elsewhere in Alabama.*

	n	C	N	T	C and N	C and T	N and T	C, N, and T	Total
Bats from Samford Hall									
Eptesicus fuscus	88	0	2	18	0	0	0	0	20
Tadarida brasiliensis	105	0	25	2	1	0	0	0	28
Total	193	0	27	20	1	0	0	0	48
Bats from elsewhere in Alabama									
Eptesicus fuscus	40	0	1	11	0	0	2	0	14
Lasiurus borealis	10	1	3	1	0	2	1	0	8
Lasiurus cinereus	1	0	0	0	1	0	0	0	1
Lasiurus seminolus	3	0	0	0	0	3	0	0	3
Myotis austroriparius	11	0	2	4	0	2	0	0	8
Myotis septentrionalis	1	0	0	1	0	0	0	0	1
Nycticeius humeralis	15	0	3	0	2	0	0	1	6
Pipistrellus subflavus	45	0	2	29	1	0	0	0	32
Corynorhinus rafinesquii	1	0	0	0	0	0	0	0	0
Tadarida brasiliensis	4	0	0	0	0	0	0	0	0
Total	131	1	11	46	4	7	3	1	73
Bats from Samford Hall and elsewhere in Alabama									
Eptesicus fuscus	128	0	3	29	0	0	2	0	34
Tadarida brasiliensis	109	0	25	2	1	0	0	0	28
Grand Total	324	1	38	66	5	7	3	1	121

($G = 92.17 >> X^2_{0.05[2]}$), or cestode-nematode ($G = 42.80 >> X^2_{0.05[2]}$). Individual bats typically host a single taxon of parasite, but dual-taxa parasitizations have been recorded for *L. cinereus* in Maryland (Tromba, 1952) and British Columbia (Webster and Casey, 1973), *N. humeralis* in Indiana (Pistole, 1988), *E. fuscus* in Missouri (Adams and Morris, 1971), and *E. fuscus* and *T. brasiliensis* in Cuba (Barus and del Valle, 1967). Pistole (1988) indicated that *E. fuscus, L. borealis, M. septentrionalis,* the little brown bat *(Myotis lucifugus),* and the Indiana myotis *(Myotis sodalis)* can be parasitized by more than one taxon of helminth.

That bats often do not harbor parasites from more than one taxon is expected because some bats are dietary specialists (Buchler, 1976; Kunz, 1973). Parasites are obtained from what bats eat (Holmes, 1964; Phillips, 1966) and being a dietary specialist may predispose a bat to become parasitized by only the type of helminth that uses the prey items as intermediate hosts. Although many species of insectivorous bats have a diversified diet that includes several orders and families of insect prey, some species feed selectively on one type of prey and show specificity to foraging habitat. Thus, mayfly (Ephemeroptera) and beetle specialists, such as *M. lucifugus* (Anthony and Kunz, 1977; Buchler, 1976), and moth (Lepidoptera) specialists, such as *L. borealis, L. cinereus* (Kunz, 1973; Ross, 1967), and *T. brasiliensis* (Ross, 1967) may be less likely to have dual-taxa parasitizations than *E. fuscus,* which has generalistic feeding habits (Kunz, 1973; Ross, 1967). *L. borealis, L. cinereus,* and *M. lucifugus* also exhibit site-specificity of foraging habitats (Kunz, 1973), whereas *E. fuscus* is not site-specific (Furlonger et al., 1987; Geggie and Fenton, 1985; Kunz, 1973).

The only bat in our study that had cestodes, nematodes, and trematodes was a female *N. humeralis* (Table 2) from Fort Rucker, Dale Co. Of parasites of nine adult female and six juvenile *N. humeralis* from Iowa, six adults and one juvenile had cestodes, seven adults and four juveniles had nematodes, and one adult had a trematode (Ubelaker and Kunz, 1971). Two of the taxa must have overlapped and all three may have occurred in one bat. The three taxa do not overlap in any other report of parasites in *N. humeralis* (Alicata, 1932; Chandler, 1938; Chitwood, 1937; Macy and Rausch, 1946; McIntosh, 1932; McIntosh and McIntosh, 1935; Pistole, 1988; Ubelaker, 1966, 1970). Relatively little is known about the biology of *N. humeralis* (Harvey, 1992; Watkins, 1972), but this species may have a wide range of prey types.

Frequencies of parasitism in *E. fuscus* (22.7%) and *T. brasiliensis* (26.7%) from Samford Hall, Auburn University, were not significantly different ($G = 0.40$, $d.f. = 1$, $P = 0.53$), but frequencies of occurrence of nematodes and trematodes were significantly different between these species ($G = 37.8$, $d.f. = 1$, $P < 0.01$). Of the 20 *E. fuscus* that were parasitized, 10.0% ($n = 2$) had nematodes and 90.0% ($n = 18$) had trematodes (Table 2). Percentages of nematodes and trematodes were opposite for *T. brasiliensis*; 92.8% ($n = 26$) of the 28 parasitized bats had nematodes and 7.1% ($n = 2$) had trematodes (Table 2). Holmes (1964) and Ubelaker (1970) reported that *E. fuscus* is host to more species of trematodes than *T. brasiliensis* and attributed this to differences in feeding habits. Holmes (1964) noted that *T. brasiliensis* feeds heavily on moths and <1% of the diet is composed of insects with aquatic larvae. Conversely, *E. fuscus* primarily feeds on beetles, but >15% of the diet is composed of insects with aquatic larvae. *E. fuscus* also feeds on water scavenger beetles (Coleoptera: Hydrophilidae), mayflies (Ephemeroptera), stoneflies (Plecoptera), caddisflies (Trichoptera), nerve-winged insects (Neuroptera—Hamilton, 1933), predatory diving beetles (Coleoptera: Dytiscidae—Phillips, 1966), dixa flies (Diptera: Dixidae—Ross, 1967), tipulid flies (Diptera: Tipulidae), and midges (Diptera: Chironomidae—Whitaker, 1972). All of these insects have aquatic larvae, and metacercaria of trematodes that infect bats have been found in larvae of midges (McMullen, 1937), caddisflies (Brown, 1933; M. C. Hall, 1929; Knight and Pratt, 1955), stoneflies (J. E. Hall, 1960; M. C. Hall, 1929), and mayflies (Etges, 1959; J. E. Hall, 1960; M. C. Hall, 1929). Conversely, Hamilton (1933) examined 2,200 fecal pellets from *E. fuscus* and found no lepidopteran remains, and Whitaker (1972) found that Lepidoptera accounted for only 4.5% of the diet of 184 *E. fuscus.*

The source of the helminth fauna of *T. brasiliensis* from Samford Hall, Auburn University, is more difficult to explain than that of *E. fuscus.* Life cycles of gastrointestinal nematodes from chiropterans have not been described (Blankespoor and Ulmer, 1970; Ubelaker, 1970), but there are no accounts of nematodes that have lepidopterans as intermediate hosts (Skrjabin et al., 1952, 1954; Yamaguti, 1961). Beetles often serve as intermediate hosts for nematodes parasitic in other mammals (Kinsella, 1991; Morgan and Hawkins, 1951; Ubelaker, 1970). However, *T. brasiliensis* feeds almost exclusively on moths, and not beetles (Bailey, 1931; Holmes, 1964; Ross, 1967; Storer, 1926). There are at least three possible explanations. First, there may be nematodes that have lepidopterans as intermediate hosts. Second, *T. brasiliensis* is not the moth specialist that the literature indicates. Third, the findings in our study are due to sampling bias; 96.3% (*n* = 109) of *T. brasiliensis* examined by us were collected from one location (Samford Hall, Auburn University). The third possibility may be most likely because *T. brasiliensis* harbors spiurid nematodes (Martin, 1976; Specian and Ubelaker, 1976), which use cockroaches (Blattodea) as intermediate hosts (Specian and Ubelaker, 1976; Ubelaker, 1970). There is a large population of cockroaches on the campus of Auburn University.

Different species of bats from the same collection localities can have dissimilar parasite loads. Font (1978) reported that ca. 80% (*n* = 35) of *M. lucifugus* he examined from Wisconsin harbored a new species of lecithodendriid trematode, *Ototrema schildti.* However, none of the *E. fuscus* (*n* = 15) from the same collection localities were parasitized by *O. schildti.* According to Font (1978), *E. fuscus* is either an unsuitable host for this species of trematode or it does not feed upon insects that have the infective stage. Webster and Casey (1973) found that *E. fuscus* (*n* = 24) and *M. lucifugus* (*n* = 31) from the same three study sites in British Columbia had little overlap in parasites. Only four of the 12 species of helminths that occurred in *E. fuscus* and *M. lucifugus* were found in both species. There were five species of trematodes that occurred in 15 (62.5%) *E. fuscus* compared with three species occurring in six (19.4%) *M. lucifugus*; two species of trematodes were found in both *E. fuscus* and *M. lucifugus.* Nematodes were represented by two species in 4 (16.7%) *E. fuscus* and three species in 11 (35.5%) *M. lucifugus*; two species of nematodes were shared. One species of cestode was present in one (4.2%) *E. fuscus* and another species was present in two (6.4%) *M. lucifugus* (Webster and Casey, 1973). Webster (1971) examined *T. brasiliensis* (*n* = 15) from a cave in Jamaica and found two species of trematodes in 12 (80.0%) bats and one species of nematode in 9 (60.0%) bats. Parnell's leaf-lipped bats (*Pteronotus parnelli*; *n* = 6) from the same cave did not have trematodes, but was parasitized by three species of nematodes, none of which occurred in *T. brasiliensis.* There also was no overlap in parasites in MacLeay's leaf-lipped bats (*Pteronotus macleayi*; *n* = 29) and *P. parnelli* (*n* = 6) from another cave in Jamaica. These two species of bats failed not only to have overlapping species of parasites, but *P. macleayi* had only trematodes and *P. parnelli* had only nematodes (Webster, 1971).

Of the parasitized bats in our study, 63 (52.1%) were males and 58 (47.9%) were females; frequency of parasitism did not differ by sex ($G = 2.31$, *d.f.* = 1, $P = 0.13$). Sex-specific differences in frequency of parasitism were not apparent for *E. fuscus* ($G = 0.01$, *d.f.* = 1, $P = 0.95$), *P. subflavus* ($G = 1.25$, *d.f.* = 1, $P = 0.26$), or *T. brasiliensis* ($G = 0.68$, *d.f.* = 1, $P = 0.41$; Table 3). Nickel and Hansen (1967) reported that 18 (27.7%) male and 7 (10.8%) female bats were parasitized. Their study included *E. fuscus* (*n* = 4), *P. subflavus* (*n* = 10), and *T. brasiliensis* (*n* = 9), but numbers of males and females of each species were not given. In their study, a male and female *E. fuscus* each had trematodes, one female *P. subflavus* had trematodes, one male *T. brasiliensis* had trematodes, and one female *T. brasiliensis* had nematodes.

Table 3.—*Frequencies of parasitism in three species of bats in Alabama based on sex.*

Species	Sex	Parasitized	Unparasitized	Total
Eptesicus fuscus	Male	11	31	42
	Female	23	63	86
Pipistrellus subflavus	Male	25	8	33
	Female	7	5	12
Tadarida brasiliensis	Male	12	42	54
	Female	16	39	55
Total		94	188	272

Contingency table analysis of their data failed to reveal a significant difference between these frequencies ($G = 0.03$, $d.f. = 1$, $P = 0.86$). Because of small samples analyzed to date, significant differences between sexes may be detected in future research. Anthony and Kunz (1977) demonstrated that female *M. lucifugus* exhibited a significant preference for beetles and mayflies on a seasonal basis. Unfortunately, no other investigations of parasite faunas included comparisons between sexes for any species of bats, and data from these studies do not allow extraction of such information.

Peak prevalence of parasites for *E. fuscus* from Samford Hall, Auburn University, was in April when 40.0% ($n = 5$) were hosts to helminths. Prevalence declined monthly thereafter until it reached 8.3% ($n = 12$) in October (Fig. 1a). Prevalences for *T. brasiliensis* from Samford Hall had a more irregular distribution. Greatest prevalence was in November when 50.0% ($n = 12$) had parasites and lowest prevalence was in September when none of the bats ($n = 12$) were parasitized (Fig. 1b). Coggins et al. (1982) found that *M. lucifugus* in Wisconsin had lowest prevalences of parasites in summer (July and August) and highest prevalences in spring (April, May, and June) and autumn (September and October). However, Blankespoor and Ulmer (1970) and Nickel and Hansen (1967) found that prevalences were low in spring and increased until the bats entered hibernation in autumn. The authors of both studies suggested that bats lost their parasites during hibernation and were reinvaded by parasites when they came out of hibernation (Blankespoor and Ulmer, 1970; Nickel and Hansen, 1967). According to Coggins et al. (1982), this strategy would work only for parasites of bats that did not undergo long (>3 months) periods of hibernation. Because bats in Wisconsin hibernate for nearly 8 months, the months of activity are not long enough to ensure successful completion of life cycles of parasites (Coggins et al., 1982). Coggins et al. (1982) maintain that parasites of bats from northerly latitudes are adapted to overwintering in their definitive host and not the intermediate host as do most helminths. One would expect prevalences in *E. fuscus* and *T. brasiliensis* in Alabama to follow the scenario proposed by Blankespoor and Ulmer (1970) and Nickel and Hansen (1967). Instead, prevalences in *E. fuscus* were highest in spring and lowest in autumn, and prevalences in *T. brasiliensis* failed to follow a discernable pattern.

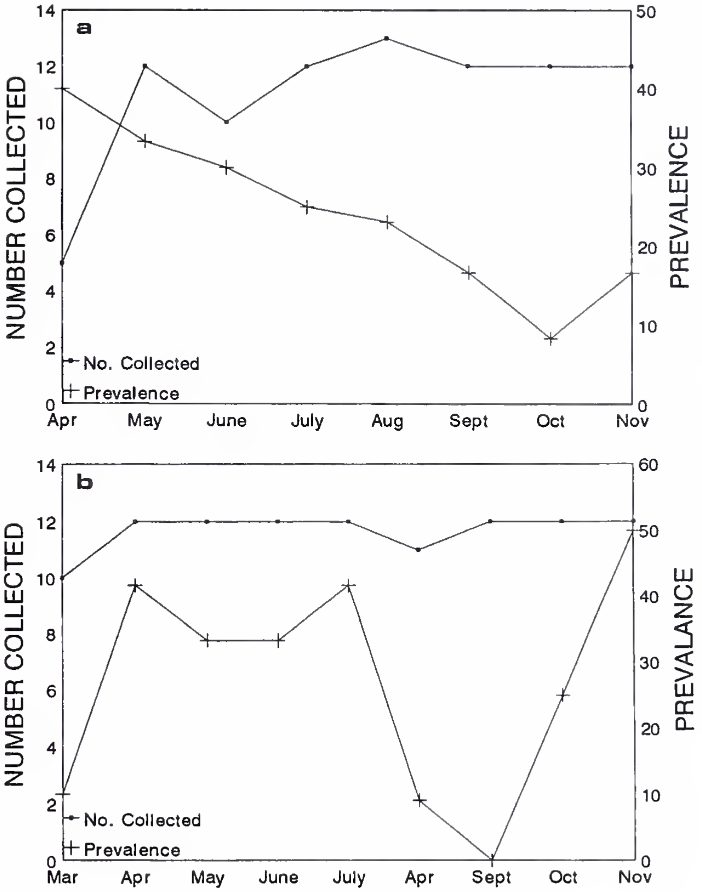

Fig. 1.—Number of a) *Eptesicus fuscus* and b) *Tadarida brasiliensis* from Samford Hall, Auburn University, Lee Co., Alabama, examined and prevalence of parasites by month during 1990.

Scanning electron micrographs were taken of at least one cestode from every bat that harbored cestodes; a trematode from one *L. borealis* also was micrographed. Cestodes from *L. seminolus* did not appear to have a rostellum or armed suckers, which suggests that they belong to the Anoplocephalidae (Schmidt, 1986). It was not apparent whether the cestode from *M. austroriparius* had a rostellum or whether the suckers were armed. The cestode from *P. subflavus* appeared to have a rostellum and unarmed suckers, which suggested that it was a member of the Hymenolepididae (Schmidt, 1986). The trematode from *L. borealis* appeared to be a distome, because it had an oral sucker and an acetabulum on the mid-ventral surface (Schmidt and Roberts, 1989). Measurements were not taken of potentially diagnostic features because parasites were fixed in situ. This fixation method causes a layer of mucus to become affixed to specimens, often distorts specimens by causing them to contract, and may result in diagnostic features such as armature becoming invaginated (M. H. Pritchard, pers. comm.; Pritchard and Kruse, 1982). Consequently, diagnostic features were not visible or were distorted such that there was a significant probability of reaching erroneous taxonomic conclusions. However, Hymenolepididae and Anoplocephalidae are the only families of cestodes to be reported in bats from the United States (Ubelaker, 1970), and the trematodes of bats in the United States are distomes (Schmidt and Roberts, 1989; Yamaguti, 1958).

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APPENDIX I

Specimens Examined

Eptesicus fuscus—Butler Co.: Georgiana, bridge on state road 106 where it passes over West Railroad Avenue (mile marker 12) (6 males, 19 females). *Lee Co.*: Auburn (0, 1); Auburn University, attic of Samford Hall (28, 60); Opelika, 1103 Collinwood Drive (5, 6); Opelika, inside duplex at 709 North 8th Street (1, 0). *Morgan Co.*: Talucah, Talucah Cave (2, 0).

Lasiurus borealis—Dale Co.: Fort Rucker, Ech Lake (0, 3); Fort Rucker, Girl Scout Camp (1, 3). *Lee Co.*: Auburn University, Ralph B. Draughon Library (1, 0); Flake Creek at county road 65, 0.3 mile from state road 169 (0, 1); Pond on state road 169, 0.3 mile from county road 65, teardrop-shaped pond (0, 1).

Lasiurus cinereus—Lee Co.: Farm pond 0.98 mile from state road 169 on county road 81 (1, 0).

Lasiurus seminolus—Dale Co.: Fort Rucker, Ech Lake (0, 1); Fort Rucker, Girl Scout Camp (0, 1); Fort Rucker, headquarters (1, 0).

Myotis austroriparius–Conecuh Co.: Hodges Cave (1, 0); Sanders Cave, 3 miles NW Brooklyn (2, 0). *Covington Co.*: Rock House Cave, 7 miles NE Florala (1, 0). *Monroe Co.*: Locklin Cave, T6N R5E Section 4 (4, 0); Locklin Cave, 5 miles W Perdue Hill (3, 0).

Myotis septentrionalis—Franklin Co.: 9 miles NE Red Bay on county road 88 before the Bear Creek Levee (1, 0).

Nycticeius humeralis—Dale Co.: Fort Rucker, Girl Scout Camp (3, 2). *Lee Co.*: Flake Creek at county road 65, 0.3 mile from state road 169 (1, 0); Opelika, 209 South 4th Street (Bathesda Baptist Church) (0, 3); Opelika, 403 Avenue A (0, 2); Opelika, 403 Avenue A and attic of Bethesda Baptist Church across street from 403 Avenue A (1, 3).

Pipistrellus subflavus—Butler Co.: B. C. Barganier Cave (=Rock Cave) (3, 0). *Clark Co.*: Buzzard's Den Cave, T9N R1E Section 18 (11, 0); Lion's Den Cave, 3 miles SW McEntyre (1, 0). *Conecuh Co.*: Sanders Cave, 3 miles NW Brooklyn (3, 2). *Franklin Co.*: 9 miles NE Red Bay on county road 88 before the Bear Creek Levee (5, 4); Goat Cave (=Belgreen Underground Lake), near Belgreen (2, 1). *Lee Co.*: Flake Creek at county road 65, 0.3 mile from state road 169 (1, 0); Pond on state road 169, 0.3 mile from county road 65, teardrop-shaped pond (1, 0). *Marshall Co.*: Mike's Wolff Cave, Union Grove (4, 0). *Marshall Co.*: Wolff Cave, Union Grove (0, 5). *Morgan Co.*: Talucah Cave, Talucah (2, 0).

Corynorhinus rafinesquii—Clark Co.: Buzzard's Den Cave, T9N R1E Section 18 (1, 0).

Tadarida brasiliensis—Bullock Co.: Union Springs, 304 East Hardaway (0, 1). *Butler Co.*: Georgiana, bridge on state road 106 where it passes over West Railroad Avenue (mile marker 12) (2, 0). *Lee Co.*: Auburn University, attic of Samford Hall (51, 54); Opelika, 1103 Collinwood Drive (1, 0).

DISTRIBUTION AND STATUS OF LECONTE'S FREE-TAILED BAT (TADARIDA BRASILIENSIS CYNOCEPHALA) IN ALABAMA

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Colonies of nuisance bats in Alabama were investigated 1990-1994 to determine distribution and status of LeConte's free-tailed bats *(Tadarida brasiliensis cynocephala).* Additional records were obtained from museum specimens and published literature. *T. b. cynocephala* is widely distributed throughout the southern one-half of Alabama; however, its roosts are disappearing rapidly due to outright destruction, exclusion, and bat-proofing of structures. At present, few extant colonies of this bat in Alabama are known. Bats excluded from one roost found in this study are believed to have relocated to another structure nearby.

Two subspecies of *Tadarida brasiliensis* (Brazilian free-tailed bat) occur in the United States (Barbour and Davis, 1969). The Mexican free-tailed bat *(T. b. mexicana),* found in the western United States and southward, usually migrates to Mexico in autumn, lives primarily in caves, and does not hibernate (Barbour and Davis, 1969; Wilkins, 1989). LeConte's free-tailed bat *(T. b. cynocephala),* which occurs in the southeastern United States (from eastern Texas and Arkansas to southern North Carolina), is non-migratory or migrates only short distances, is not known to inhabit caves, and spends part of winter in torpor (Barbour and Davis, 1969; Lee and Marsh, 1978; McNab, 1982; Wilkins, 1989). The ranges of these subspecies are adjacent in eastern Texas, but there is little evidence for genetic exchange between them (Carter, 1962; Owen et al., 1990). Both subspecies use man-made structures as roosts (Bailey, 1951; Barbour and Davis, 1969; Schmidly, 1991; Wilkins, 1989).

Until 1996, *T. b. cynocephala* was listed as a species of special concern by the Alabama Department of Conservation and Natural Resources (Mount, 1984) and records of its occurrence in Alabama were uncommon (Barkalow, 1939). However, Holliman (1963) indicated that *T. b. cynocephala* was found throughout Alabama and was moderately common. Jordan (1986) stated that *T. b. cynocephala* has been reported from throughout the Coastal Plain of Alabama, but no specific localities were given. Howell (1921) found a colony in Greensboro, Hale Co., in 1890. He also examined two specimens that were captured at Orange Beach, Baldwin Co., in 1912. In 1938, Barkalow (1939) obtained a specimen from a brick building on the campus of Alabama Polytechnic Institute, Lee Co., which is now Auburn University. Additional specimens also have been collected from the campus of Auburn University in recent years (Durden et al., 1992; Henry et al., 2000; Hilton and Best, 2000; Kiser, 1996). Carter (1962) secured specimens from a building in Butler, Choctaw Co., Di Salvo et al. (1969) collected 100 specimens from an attic in Tuscaloosa, Tuscaloosa Co., and Hilton and Best (2000) collected specimens from Union Springs, Bullock Co., and Georgiana, Butler Co. *Tadarida* has been recorded from Jackson Co. in northeastern Alabama, but this is considered outside the usual range (Holliman, 1963; Jordan, 1986). The purposes of this study were to determine the present distribution of *T. b. cynocephala* in Alabama and to summarize what is known about its present status.

MATERIALS AND METHODS

Data for this study were obtained from investigations of colonies of nuisance bats in Alabama from June 1990 to September 1994, from specimens deposited in the Auburn University mammal collection, and from published literature. Following inspection of several roosts, nuisance bats were excluded (evicted) using non-lethal devices (Greenhall, 1982). Size of colonies was estimated when possible prior to exclusion and at various times after exclusion.

RESULTS AND DISCUSSION

During this study, 26 roosts of *T. b. cynocephala* were located in the southern part of Alabama (Table 1; Fig. 1). Roosts were discovered in 15 counties, 10 of which were new records. Two maternity roosts (Auburn

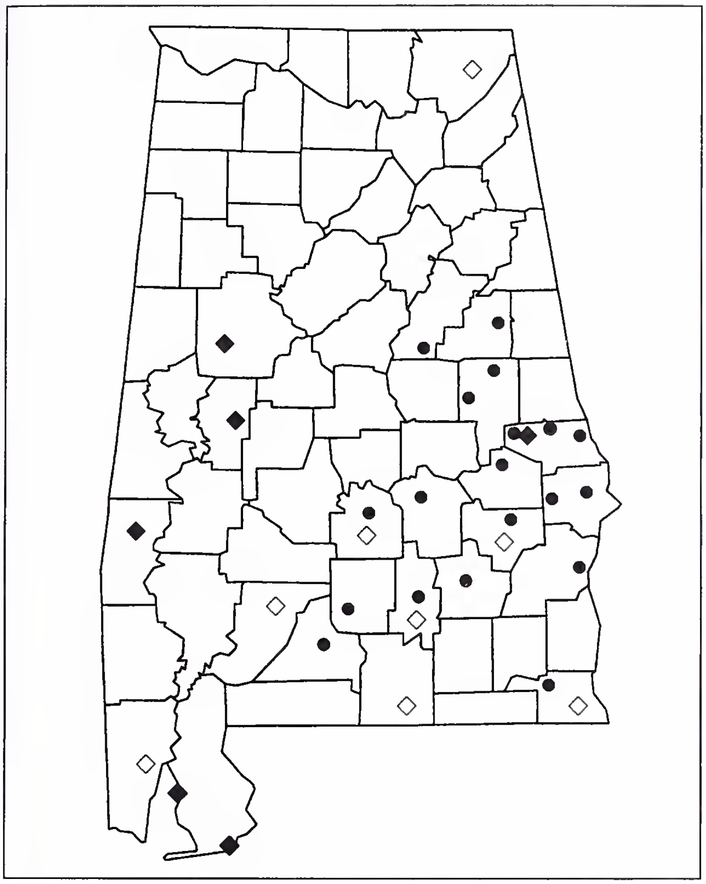

Fig. 1.—Distribution of *Tadarida brasiliensis cynocephala* in Alabama. Solid diamonds are literature records, open diamonds are county records (no specific locality given), and solid circles are new colonies of *T. b. cynocephala* located during this study.

University, Lee Co., and Dothan, Houston Co.), and one winter roost (Auburn University, Lee Co.) were located. A total of 14 literature records from 13 counties also were examined (Fig. 1); all (except the record for Jackson Co.) were located in the southern one-half of the state. These records indicate that *T. b. cynocephala* is widely distributed throughout southern Alabama. However, roosts of *T. b. cynocephala* rapidly are disappearing; 20 of 26 colonies discovered during this study were either destroyed, excluded, or were scheduled to be excluded. The status of four other colonies is unknown. Only a few extant colonies are known in Alabama at present (Table 1), although others may exist.

Tadarida b. cynocephala roosts in buildings and other man-made structures throughout the year, and is not known to use caves (Barbour and Davis, 1969). All 26 roosts I examined were located in man-made structures such as bridges, stadiums, attics, and spaces between walls, floors, or ceilings (Table 1). Most roosts located in this study occurred in masonry structures. Previous studies also have shown that *T. b. cynocephala* often selects roosts constructed of concrete or bricks (Bailey, 1951; Pagels, 1972, 1975). Masonry structures may provide stable roost temperatures during the critical maternity and torpor periods (Carter, 1962). However, Lowery (1974) and Jennings (1958) indicate that *T. b. cynocephala* in Louisiana is not averse to roosting in hollow trees, where they may be sympatric with *Nycticeius humeralis.* Hollows of trees probably served as natural roosts of these bats before the arrival of Europeans in North America and large-scale clearing of forests (Jennings, 1958).

In some cases, *T. b. cynocephala* apparently switches roosts or migrates short distances during winter; thus, precise location and nature of winter roosts can be difficult to determine (Belwood, 1992; Jordan, 1986; Kiser, 1996; La Val, 1973; Wilkins, 1989). In this study, one colony of *T. b. cynocephala* found in the expansion joints of a bridge (Georgiana, Butler Co.) were present in summer only; however, another colony was present year-round in Samford Hall at Auburn University (Durden et al., 1992; Kiser, 1996), although most had switched roosts in late autumn or winter. Other buildings on the campus of Auburn University later contained torpid *T. b. cynocephala* in winters of 1992 and 1993. However, bats from this colony also were observed foraging on warm nights during this same time period (M. T. Mendonça, pers. comm.). All 26 specimens examined from the Auburn University mammal collection (20 males, 5 females, 1 unknown sex, collected in Auburn and Opelika, Lee Co., 1942-1986), were taken January-April, confirming the existence of other winter roosts. Clearly, further studies of winter habits and migratory patterns of this sub-species are needed.

As large colonies in buildings generally constitute a nuisance, *T. b. cynocephala* particularly is vulnerable to roost destruction, vandalism, harassment, or deliberate killing. Thus, large segments of the population can be lost in a short period of time (Belwood, 1992). For example, the only permanent colony of this bat known in Alabama (i.e., in which breeding and overwintering occurred), which was located on the campus of Auburn University, recently was excluded from one building and destroyed in another (Henry et al., 2000).

Although exclusion and bat-proofing (when bats are

Table 1.—*Recent occurrences of* Tadarida brasiliensis cynocephala *in Alabama.*

County	Site	Current status	Comments
Barbour	Church building, Eufaula	Unknown, scheduled for exclusion autumn 1993	Investigated by F. Boyd in summer 1993; >1,000 bats in ceiling and attic of pre-civil war structure of wood-plaster board construction
Barbour	Doctor's office/ residence, Eufaula	Active	Investigated by F. Boyd and G. Gardner in summer 1993; 5,000-10,000 bats in attic
Bullock	Bullock Co. Courthouse, Union Springs	Excluded ca. 1990	Investigated by C. D. Hilton 16 November 1990; unknown number present; bats may have relocated to adjacent church
Bullock	Private residence, Union Springs	Unknown	Investigated by C. D. Hilton 16 November 1990; one female collected
Butler	Highway bridge, Georgiana	Active	At times, several hundred were in expansion joints with *E. fuscus;* reported to be a satellite colony from nearby high school; summer roost only
Clay	Bank building, Lineville	Unknown, scheduled for exclusion autumn 1994	Unknown number present in attic of old house (built in 1904) that was converted into a bank
Conecuh	Highway bridge, Evergreen	Scheduled for exclusion autumn 1994	Investigated by F. Boyd 24 June 1994; >2,000 in expansion joints of bridge
Crenshaw	Brantley Elementary School, Brantley	Excluded 1993	Investigated by F. Boyd 1993; ca. 600-800 with *E. fuscus* in roof of new primary building; bats may have relocated to nearby high school
Houston	Old Houston Hotel, Dothan	Excluded winter 1992	On 10 June 1992, >1,600 counted with ca. 100 *E. fuscus* in copper flashing on outside of brick building
Houston	Private residence, Dothan	Excluded August 1993	On 12 July 1993, ca. 200 bats in attic of house with *N. humeralis;* two females were lactating
Lee	Samford Hall, Auburn University	Excluded May 1994	Ca. 700-1000 bats present with *E. fuscus* in attic of brick building in summer, some still present on campus after exclusion
Lee	Biggin Hall, Auburn University	Destroyed winter 1994	Ca. 400 bats overwintering in brick walls with *E. fuscus* in December 1994; part of Samford Hall colony

Table 1.—*continued*

County	Site	Current status	Comments
Lee	Church building, Opelika	Unknown, scheduled for exclusion	In summer of 1992 and 1993, ca. 100-300 with *E. fuscus* and *N. humeralis* in brick-cinder block walls of two separate buildings
Lee	Private residence, Auburn	Excluded autumn 1992	In summer 1992, ca. 200 present inside brick wall with *E. fuscus*
Lee	Private residence, Valley	Unknown, scheduled for exclusion	On 1 June 1993, one was observed among *E. fuscus* and a maternity colony of *N. humeralis* in attic of house
Lee	Private residence, Opelika	Unknown	One male collected by C. D. Hilton 27 June 1990
Lowndes	Lowndes Co. Courthouse, Hayneville	Excluded autumn 1992, bats returned, then excluded in autumn 1993	In summer 1992, ca. 200 present in cinder-block and brick walls of attic attic with *E. fuscus* and *N. humeralis*
Macon	Macon Co. High School, Tuskegee	Excluded 1992, bats returned, excluded in 1993	In summer 1992, ca. 500 present in cinder-block wall of gymnasium
Montgomery	Apartment complex, Montgomery	Excluded autumn 1992 and 1995	In summer 1992, ca. 200 were present with *N. humeralis* in brick and cinder-block wall
Pike	Troy State University, Troy	Unknown	Unknown number reported in one or more campus buildings
Russell	Old Courthouse, Seale	Excluded autumn 1993	In spring 1992, ca. 200 were present with *E. fuscus* in brick walls and attic
Russell	Private residence, Hurtsboro	Scheduled for exclusion, autumn 1994	In June 1994, unknown number (>20) present with >100 *N. humeralis* in walls of house
Talladega	Housing project, Sylacauga	Scheduled for exclusion, autumn 1994	On 10 June 1994, unknown number were present in several two-story brick housing units with *E. fuscus*
Tallapoosa	Church building, Alexander City	About 300 killed, 1993; remainder excluded, August 1993	On 1 August 1993, >200 present with *E. fuscus* in gap between two brick buildings, and in attic of brick-cinder block building

Table 1.—*continued*

County	Site	Current status	Comments
Tallapoosa	New Site High School, New Site	Excluded September 1993	On 7 September 1993, >100 present inside brick and cinder-block walls of gymnasium on east side, at roof level
Tallapoosa	Sports complex, Alexander City	Unknown	On 2 September 1993, >100 present with *E. fuscus* in expansion joints of football stadium constructed of concrete

absent) are non-lethal methods of controlling nuisance bats, some bats may suffer indirect mortality from predation or exposure while attempting to return to the previous roost, or while searching for a new roost (L. Finn, pers. comm.). Following exclusion, bats unable to locate a suitable structure nearby may die, particularly if the exclusion is performed in winter, when fat stores are low and food is scarce. Exclusion or destruction has been the fate of nearly all colonies of LeConte's free-tailed bats discovered in Alabama in past years. Whether or not the majority of excluded bats are successful in finding new roosts and establishing new colonies is unknown at present.

Colonies of 10,000-50,000 *T. b. cynocephala* once were common in Florida, although colonies of this size now are rare (Belwood, 1992; Jennings, 1958). The attic of an old building in Baton Rouge, Louisiana, contained ca. 20,000 bats and was used as a summer roost for >35 years (Lowery, 1974). In contrast, few roosts with >1,000 LeConte's free-tailed bats have been documented in Alabama. These occurred in Auburn (Lee Co.), Dothan (Houston Co.), Eufaula (Barbour Co.), and Evergreen (Conecuh Co.). Large groups of *T. b. cynocephala* were discovered during this study in Eufaula; in summer of 1993 a church contained >1,000 individuals and a nearby residence contained >5,000 individuals. Adjacent buildings also contained bats. Most roosts located in this study had <300 individuals, and most were sympatric with *Nycticeius humeralis, Eptesicus fuscus*, or both (Table 1).

Available evidence indicates that *T. b. cynocephala* is relatively sedentary and is unlikely to move a great distance if its roost is destroyed (Carter, 1962). In two instances where roosts were destroyed, *Tadarida* successfully relocated to new structures a short distance away. Similar evidence may have been found in this study. A colony excluded from a church in Alexander City, Tallapoosa Co., in 1993, is believed to have relocated to a football stadium several kilometers away. Bats occupied the stadium 2 weeks after exclusion was completed at the church building; no previous roosting activity in the stadium was known.

Some conservation measures recently were taken to protect bats in Alabama. With the exception of napthalene, no chemicals are registered in Alabama for use in the removal of bats. Until 1996, a permit was required to remove *T. b. cynocephala* from buildings (State of Alabama Regulation 92-GF-16; Rule 220-2-92). Auburn University, following efforts made by The University of Florida at Gainesville, recently attempted to relocate a colony of *T. b. cynocephala* to a large-scale bat house. Despite repeated attempts at Auburn University, no bats occupied the bat house on a permanent basis. In 1997, an estimated 20,000 *Tadarida* used the bat house at The University of Florida as a maternity site (Kiser, 1996; Kiser and Glover, 1997).

Few data on natural history of *T. b. cynocephala* in Alabama are available, although biologists generally agree that populations have declined in recent years (Jordan, 1986). More information on habitat requirements, seasonal movement patterns, and summer and winter roosting habits of *T. b. cynocephala* in Alabama is needed. Where feasible, known roosts of *Tadarida* should be preserved. Alternate roosts, such as bat houses and bat towers, are needed, and could serve an important role in the conservation of this bat, although more research is needed to develop cost-effective designs that LeConte's free-tailed bats will use year-round. Bat houses should be placed near existing colonies before any exclusion is performed.

CONCLUSIONS

Data presented in this study demonstrate that *T. b. cynocephala* is widely established in the southern one-half of Alabama, although few extant colonies are known. The continued loss of established roosts does not bode well for Alabama's populations of *T. b. cynocephala*. Renovation of buildings, bat-proofing, and razing of old buildings (habitat loss), in addition to destruction of colonies, are responsible for the decline, although use of pesticides also may be a factor. Mortality of bats following exclusion is unknown, but should be investigated. The propensity of *T. b. cynocephala* to roost in large concentrations in buildings (where they may become a nuisance) and in a restricted number of localities poses special problems for conservation (Belwood, 1992).

Further conservation measures apparently are needed to ensure the future of Alabama's free-tailed bats. Alternate roosts, along with educating the public as to the beneficial role bats play in reducing populations of insect pests, will be important in protecting *T. b. cynocephala.*

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ECOLOGY AND CONSERVATION OF A FRONTIER POPULATION OF THE ROUND-TAILED MUSKRAT *(NEOFIBER ALLENI)*

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The round-tailed muskrat *(Neofiber alleni)* is endemic to the lower southeastern coastal plain of the United States, occurring locally in shallow freshwater wetland habitats, mainly in peninsular Florida. We report several new localities for the species in south-central Georgia. We studied the population ecology of these muskrats by quantification of habitat, live trapping, and radiotelemetry. We provided 10 years of censuses and data on individual home range and movement patterns for the population at Grand Bay, Georgia, and we challenged previous reports of round-tailed muskrats occupying only two houses and being strictly solitary. Ecological densities in this peripheral population were lower than densities reported from natural marshes in Florida, and crude densities appeared to fluctuate on a 2-year cycle. Floating mats of bog-like vegetation surrounded by open-water and emergent marsh dominated by sedges, such as *Carex* and *Eleocharis,* were the most commonly occupied habitats. We recommended controlled burning, hydroperiod management, and management of mats to increase habitat available to *N. alleni* in Georgia.

The round-tailed muskrat *(Neofiber alleni),* a semiaquatic arvicoline rodent of freshwater marshes, is a member of a monotypic genus first described in 1884. *N. alleni* previously was known only from peninsular Florida, a possibly distinct population in the panhandle (Wassmer and Wolfe, 1983), and a few localities in southeastern Georgia (Schantz and Jenkins, 1950). Pocosins and Carolina bays, which are shallow, peat-filled or muck-filled depressions common in parts of the southeastern coastal plain (Sharitz and Gibbons, 1982), provide habitat for the round-tailed muskrat. Harper (1920) documented *Neofiber* in prairie habitats on the eastern side of Okefenokee Swamp. The only other published record of the species in Georgia (Schantz and Jenkins, 1950) is an account of skulls of *N. alleni* in pellets from barn owls *(Tyto alba)* near Woodbine, Camden Co. Unlike the muskrat, *Ondatra zibethicus, N. alleni* rarely is found in open water and is nocturnal, with crepuscular peaks (Birkenholtz, 1972). Round-tailed muskrats are non-territorial and build their houses in dense clusters or colonies.

Neofiber alleni is listed as a species of special concern in Florida (Lefebvre and Tilmant, 1992) and is a threatened species in Georgia, but has no status federally. The species is locally distributed in freshwater wetlands throughout Florida and, apparently, is subject to wide fluctuations in population density. Greatest reported densities are for sugarcane fields in southern Florida, where the species may be considered a pest (Lefebvre, 1982; Steffen, 1978). On smaller natural marshes in central Florida, *N. alleni* may reach maximal densities of 250-300/ha, whereas on larger mashes (>1,000 ha), maximal densities are 50/ha (Birkenholtz, 1963). Round-tailed muskrats build small, tightly woven, dome-shaped houses from grasses, sedges, or cattails, which are attached to surfaces of floating mats of *Sphagnum,* plant roots and organic muck, or to bases of shrubs or small trees (Baker, 1889; Birkenholtz, 1972; Chapman, 1889; Harper, 1920, 1927; Tilmant, 1975). They also clip vegetation to build floating feeding platforms (Birkenholtz, 1963). However, when water levels drop, round-tailed muskrats abandon their houses and tunnel into the saturated peat substrate.

In autumn 1987, we discovered several colonies of *N. alleni* inhabiting three semi-isolated wetlands within the 5,200-ha Grand Bay wetland ecosystem (including Grand Bay Wildlife Management Area and adjoining lands) in northeastern Lowndes Co. and southeastern Lanier Co., Georgia. These three wetlands have had different management histories, and, therefore, varied in microhabitat composition. We attempted to describe the status and population ecology of populations at Grand Bay by live trapping, quantification of habitat, annual surveys by airboat and helicopter, and observation of radiotelemetered muskrats.

STUDY AREA

The three wetland habitats where colonies of *N. alleni* were found within the Grand Bay ecosystem displayed characteristics of Carolina bays (Sharitz and Gibbons, 1982), which are elliptical, peat-filled or muck-filled shallow depressions manifesting a variety of wetland vegetative types. During 1987-1988, habitats could be classified as open marsh with floating-mat vegetation (Grand Bay), shrub bog (Oldfield Bay), and chain-fern *(Woodwardia virginica)* marsh with saturated peat soil, but little open water (Rat Bay). Due to fire exclusion, shrub-bog and chain-fern habitats were succeeding toward dense-understory, quasi-terrestrial habitats in 1987. Rat Bay, a 340-ha portion of a Carolina bay that was isolated by construction of water-control dikes, was dominated by chain fern, with a thick mat of *Sphagnum* and widely scattered shrubs and small trees. The water table was at, or below, the surface in most areas. Grand Bay was a 550-ha Carolina bay with habitats ranging from open water to emergent marsh to shrub bog to pond cypress *(Taxodium ascendens)* and black gum *(Nyssa biflora)* swamp. Evidence of round-tailed muskrats was found mostly on floating mats at edges of small patches of shrub bog and near open water.

Water levels on Grand Bay, which were maintained by permanent water-control structures, were much higher than on Rat Bay; consequently, vegetative growth was higher and denser on Rat Bay, where there was little or no open water. A thick layer of sphagnum had accumulated over most of the site. A successful burn in late autumn 1987, and completion of water-control structures, allowed managers to raise and maintain water levels and, thereby, return Rat Bay to a more open, emergent, marsh habitat by 1989. Oldfield Bay (2,400 ha) was still succeeding and most of it, apparently, was abandoned by *N. alleni* during the first 6 years of the study.

MATERIALS AND METHODS

Preliminary surveys of nesting and feeding structures, and of habitat structure and plant composition, were conducted on Grand Bay and Rat Bay from late winter through summer 1988. Surveys by helicopter of suitable wetland habitats in Brooks, Thomas, Lowndes, Lanier, Berrien, Cook, and Clinch counties, Georgia, were conducted in March 1991 to try to discover additional colonies of *N. alleni.*

Characterization of habitat.—Centered on occupied areas of marsh habitat within both Grand Bay and Rat Bay, a rectangular survey grid 180 by 680 m (12.24 ha) with 350 stations spaced 20 m apart was established in each wetland. Using a stratified-random procedure, we chose 48 stations at each of the two sites for a modified point-quarter survey (Müeller-Dombois and Ellenberg, 1974) of all plants. At each station, four 1-m^2 Daubenmire plots were located by a random procedure near each station, and four 10-m surface-cover transects radiated from the station marker at random compass directions, but at right angles to each other. Number of stems of each species of plant was recorded, as was depth of standing water and average height of vegetation. For cover transects, a tape scored on 0.1-m intervals was used to estimate percentage coverage of the following: 1, open water; 2, open floating mat or mud flat; 3, vegetated floating mat; 4, peat soil; 5, emergent vegetation; 6, tree or shrub. Species name of any tree or shrub whose branches overlaid the tape or whose trunk came within 0.1 m of the tape was recorded. All habitat data were collected in June and July 1988.

Live trapping.—Preliminary attempts to live-trap round-tailed muskrats on the three Grand Bay habitats were made in winter 1987-1988, and again in summer 1988. We used single-entry, Tomahawk 201, wire-cage live-traps, Fitch live-traps, and Gregerson snares (size 0) placed around exposed plunge holes. Beginning in later winter 1991, and continuing through summer, we again attempted to live-trap rats, but this time only in Grand Bay using Haguruma live-traps (Honolulu Sales, Ltd., Honolulu, HI). Traps were baited with halved golden delicious apples, and natural vegetation (grasses, sedges) was placed over the floor of the wire-mesh trap surrounding the treadle.

Radiotelemetry.—In 1991, live-captured *N. alleni* from Grand Bay were implanted within 24 h with 7-g radiotransmitters (Telemetry Systems, Inc., Mequon, WI) sealed in epoxy resin and equipped with magnetic switches. Frequencies of radiotransmitters were 164-168 KHz. Animals were sedated with an intramuscular injection of ketamine hydrochloride at 0.05 cc/100 g of body weight, which generally took effect in 5 min and lasted for 20 min. Radiotransmitters were soaked for 24 h prior to surgery in a povidone-iodine solution, and were implanted intraperitoneally between the rectus abdominus and external oblique muscles through a 30-mm incision. A 0.1-cc injection of penicillin was given following surgery. Each animal was released at its point of capture after a 24-h recovery and observation period.

A Telonics TR-2 receiver and 3-element Yagi antenna were used to locate muskrats after release, using an airboat as observation points. Each animal was located at least twice each day; around dawn and dusk, and some animals were tracked continuously throughout the night. All houses of round-tailed muskrats and occupied mats were mapped in reference to the Grand Bay grid, and each telemetry fix was recorded in terms of distance and compass direction from the nearest house. Each muskrat was followed daily until its signal disappeared, it was found dead, or a loose radiotransmitter was found. As an estimate of area of home range, Minimum Convex Polygon (MCP; Bergstrom, 1988) was calculated for all telemetered animals for which eight or more different locations were recorded.

RESULTS

Populations of *N. alleni* at Grand Bay represent a range extension of ≥72 km north and 80 km west of previously reported localities in northern Florida and southeastern Georgia, respectively (Fig. 1). The closest distance of these colonies to any published locality for *Neofiber* is 58 km NNE Madison, Madison Co., Florida (Hall, 1981). In 1991, surveys conducted by helicopter of all likely habitats in seven counties in south-central Georgia resulted in discovery of one additional colony of 13 houses in Brooks Co., 2 km N Florida state line (13 km SSE Quitman). Several other small colonies were observed just across the state line in Madison and Hamilton counties, Florida. Colonies that previously were reported from southern Thomas Co. (W. Baker, pers. comm.) and southwestern Lowndes Co. (T. Hon, pers. comm.) were not found. In 1996, a large colony with 146 active houses, not seen in 1991, was discovered in Bowen Mill Pond, 5 km W Quitman, Brooks Co.

Houses and other structures.—In 1987-1988, in Grand Bay and Oldfield Bay, *N. alleni* built conspicuous houses woven from *Carex* or other sedges and anchored to either a floating mat or the base of a shrub. Although numerous inactive houses remained in Rat Bay, by autumn 1987, the water table was below the surface, and muskrats tunneled directly into the sphagnum mat, rather than build houses. Houses typically were constructed of the sedge *Carex striata* (=*walteriana*), which usually grew near houses or tunnels. Blades of slender spikerush *(Eleocharis)* also were sometimes used. Houses were ca. 25-38 cm tall, 30 cm wide at the base, and dome-shaped. Inside, there was a medial nesting or feeding platform and two lateral plunge holes beginning just above water level and ca. 5-7 cm in diameter. In two or three active houses that were examined on Grand Bay in 1991, one of the plunge holes went straight down into the water below the mat, while the other curved and extended horizontally through the mat. Several plunge holes usually were found on larger mats that contained active houses; these may have connected with horizontal tunnels through the mat or led to the water below. Feeding platforms were areas ca. 20 cm wide that were cleared of growing vegetation, exposing the peat or muck, and usually were located close to the edge of the mat. Plant fragments in evidence around feeding platforms included roots of *Lachnanthes* and Xyris, stems of *Eleocharis* and *Carex,* and seedheads of *Lachnanthes* and *Carex.*

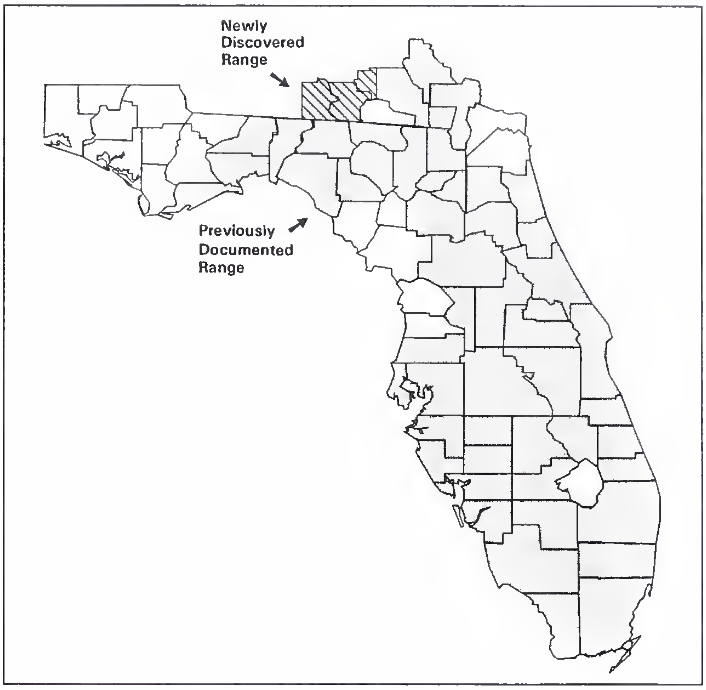

Fig. 1.—Map of Florida and southern Georgia showing distribution by county of *Neofiber alleni,* as previously reported and as newly discovered (adapted from Wassmer and Wolfe, 1983)

Most construction of new houses was observed during March and April. Old houses were repaired with fresh blades of green sedge *(Carex* and *Eleocharis)* that were conspicuously woven among the brown blades of the existing house. Before emergent vegetation started its rapid growth and wetlands greened up was the best time to census houses aerially. Many abandoned houses were seen on occupied mats; many of these had been taken over by swarms of fire ants *(Solenopsis),* and were not

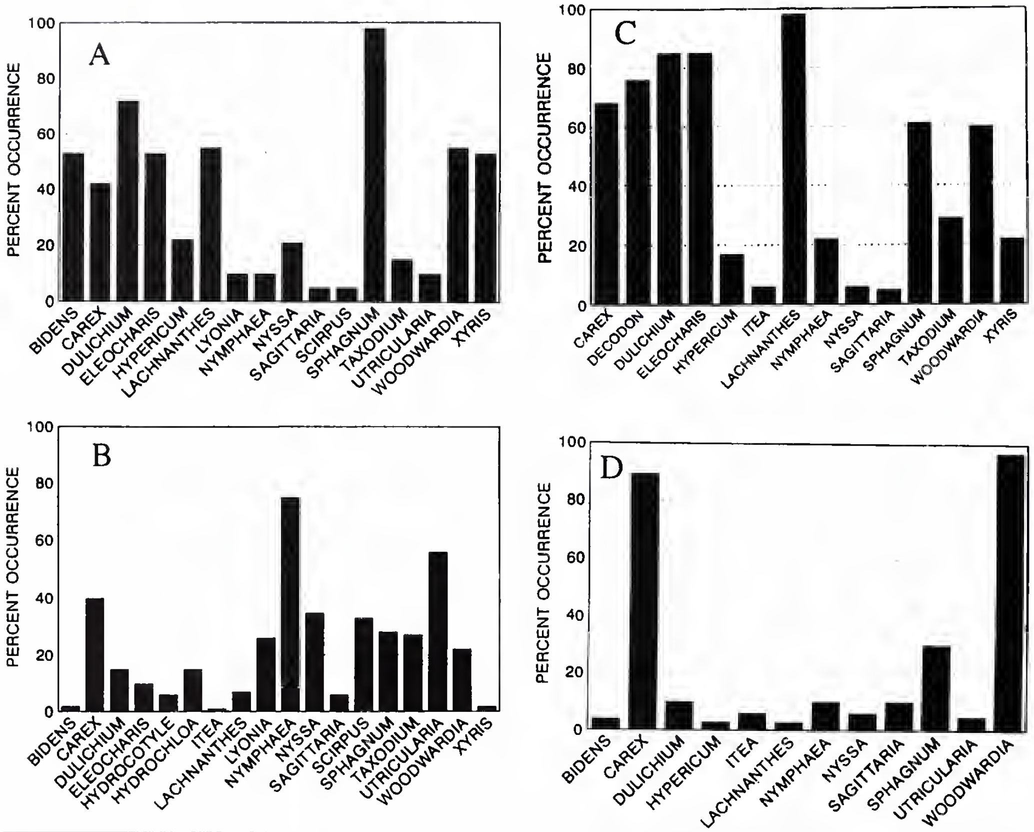

Fig. 2.—Percentage occurrence of herbaceous and woody plants of various species on 192 1-m2 Daubenmire plots randomly placed in four plant-community types in Grand Bay, Georgia, in decreasing order of suitability as habitat for *Neofiber alleni*: a) floating-mat bog/marsh; b) mixed emergent marsh; c) sledge marsh; d) chain-fern marsh.

counted during surveys conducted by airboat and helicopter in spring.

Characterization of habitat.—In summer 1988, Rat Bay had a thick and continuous mat and little or no standing water (mean height of water, 0.19 cm; minimum, 0; maximum, 5.0). There were two dominant plant-community types in Rat Bay; sedge emergent marsh (27% coverage) and chain-fern emergent marsh (73% coverage). In the sedge emergent community, the wetland grass *Lachnanthes caroliniana* (redroot) was the most dominant species, and four taxa of sedges (Cyperaceae); *Carex striata, Eleocharis, Dulichium arundinaceum,* and *Cyperus erythrorhizos,* along with the semi-woody perennial *Decodon verticillatus,* were codominant (Fig. 2c). *Sphagnum* and *Woodwardia virginica* (chain-fern) also were encountered frequently. Chain-fern habitat had much lower species equitability and was dominated by *W. virginica* and *L. caroliniana* (Fig. 2d). Sedge marsh at the time of low water levels was a more mesic habitat, having a substantial layer of sphagnum and greater density of shrub and tree roots. Plunge holes and freshly excavated organic matter were noted mainly in sedge areas. We presume that *N. alleni* selected sedge areas preferentially because of both moisture conditions and greater abundance of natural foods. Mean height of vegetation at Rat Bay under these low water levels was higher and less variable (mean, 93.6 cm; minimum, 67.7; maximum, 142.9) than Grand Bay (mean, 54.9 cm; minimum, 0; maximum, 110).

The Grand Bay site was more diverse due to much higher water levels (mean, 62.35 cm; minimum, 47.5; maximum, 85.1) and included four distinct habitat types. Mixed emergent marsh (25% coverage) was dominated by fragrant water lily *(Nymphaea odorata)* and bladderwort (*Utricularia;* Fig. 2b); other species were limited to floating mats or tree and shrub islands. *Nymphaea* would have been more dominant had it not been for prior treatment of the open-water areas of Grand Bay with the herbicide Sonar (Dow Elanco Co., Harbor Beach, MI), which selectively killed water lilies. Sedge emergent marsh (32% coverage) included areas of more extensive vegetation, which probably represented old floating mats that had coalesced and had been colonized for a longer time, displaying a greater abundance and diversity of plants. In this habitat, *Carex* and *Scirpus* were more abundant than in more open habitat, as were small black gum and pond cypress trees. Because this habitat contained portions of deep, open water, *Carex* had relatively low percentage occurrence (Fig. 2c).

Floating-mat communities (20% coverage) usually were covered by herbaceous and shrubby growth. *Carex, Lachnanthes caroliniana, Xyris,* and *Lyonia ludida* were common (Fig. 2a), but these areas also exhibited 50-80% open water. True floating-mat community had the greatest diversity of plant species of the four habitat types and was the habitat where houses, plunge holes, and feeding platforms of *N. alleni* most often were found. Although vast expanses of chain-fern marsh (Fig. 2d) were found on the edge of Grand Bay, it covered 25% of sampling grids and apparently was used little, or not at all, by *N. alleni.*

The area of Grand Bay where houses and other evidence of *Neofiber* were found 1988-1994 was an ecotone between mixed emergent marsh and dense chain-fern marsh and was where floating mats and sedge emergent marsh (with scattered small trees and shrubs) were found. This ecotonal area constituted suitable habitat for *N. alleni* in Grand Bay and covered an area of 34 ha, on average, throughout the study.

Surveys of houses.—In spring and summer 1988, 67 houses were located by airboat in Grand Bay; 32% of these were located in three areas of high concentration or colonies. Of the area of available habitat sampled in Grand Bay (34 ha), <25% was used by *N. alleni* in 1988. In 1989 and 1990, number of houses in the area increased gradually (Fig. 3). In 1990, houses were surveyed both by airboat and helicopter, and we found 20% more houses during the helicopter survey than during the airboat survey. In subsequent years, only surveys by helicopter were done. Numbers of houses increased from 1991 to 1992, declined in 1993, and recovered in 1994. The increase in 1992 may have been due to long-term effects of treatment in 1988 of fragrant water lily with aquatic herbicide, which produced a massive kill. After a few years, this substantial amount of partially decayed biomass floated to the surface, producing new mats. Many of the new houses in 1992 were built on new mats in an area of Grand Bay that previously had been mixed emergent marsh dominated by fragrant water lily.

Decline in number of houses in 1993 may have been an anomaly due to a severe winter storm just prior to the census. Perhaps, many houses were obliterated by wave action or hidden from aerial view by debris. In fact, several houses used by muskrats with radiotransmitters in 1991 apparently were still in use in February 1994. However, following establishment and colonization of new mats by 1992, fluctuation in the census of houses suggested a 2-year cycle. Oldfield Bay was surveyed only during the last 4 years of the study and also showed a possible 2-year cycle, with trends reciprocal with those of Grand Bay (Fig. 3).

Using an index of 2.2 houses/round-tailed muskrat (Birkenholtz, 1963) and our counts of active houses, the population in Grand Bay ranged from 36 to 108 animals. Given that there was 34 ha of suitable habitat in the inhabited portion of Grand Bay, we estimated that population density ranged from ca. 1 to ca. 3 muskrats/ha. During the 3 years in which Oldfield Bay was surveyed, population estimates ranged from 23 to 155 round-tailed muskrats.

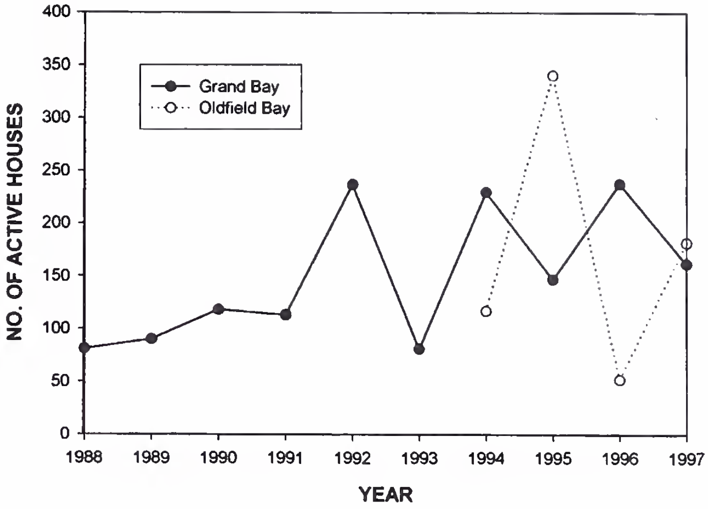

Fig. 3.—Number of active houses of *Neofiber alleni* counted from a helicopter in early spring on Grand Bay (solid) and Oldfield Bay (dashed), Georgia. Surveys in 1988 and 1989 were conducted by airboat and their results adjusted upward by 20%; all subsequent surveys were conducted by helicopter.

Live trapping.—Our attempts at live trapping in 1987 and 1988 proved labor-intensive and ineffectual, yielding only one capture in >800 trap nights using Tomahawk and Fitch traps and snares. Other species that were captured frequently in or near dwellings and tunnels of *N. alleni* included *Oryzomys palustris, Sigmodon hispidus,* and *Peromyscus gossypinus.* The latter two species were encountered most frequently in Oldfield Bay where houses had little evidence of recent work and where floating mats had coalesced into continuous expanses of dense, wet-savannah habitat, dominated by grasses and small trees and shrubs.

In 1991, we began using Haguruma live traps, and although trap success was still low, it was greater than in previous attempts. Activity of round-tailed muskrats on Grand Bay was relatively high in late winter through early summer and declined in late summer. A total of 15 captures of eight individuals was made March-August 1991 (2,790 trapnights with Haguruma traps). Six were adult males and two were adult females. Five of the six

Table 1.—*Radiotelemetry data for eight* Neofiber alleni *from Grand Bay, Georgia, 1991.*

Muskrat	Sex and reproductive condition[a]	Mass (g)	Number of traps and telemetry locations	Number of days observed	Number of mats occupied	Number of houses occupied	Size of home range (m^2)	Maximum dimension of home range (m)	Fate
LD	M+	276	67	55	5	10	58 (activity areas) 130 (plus movement corridor)	72	lost signal
ME	M+	249	10	7	1	2	20	7.5	predation by alligator
CU	M+	265	8	7	1	4	13	7.5	predation by owl
JA	F+	242	6	5	2	3			predation by alligator
JR	M	239	5	2	2	2			lost signal
CP	M+	211	7	1	1	1			lost signal
PP	M+	304	3	1	1	1			died in trap
NO	F	201	2	2	1	2			found dead

[a] A + indicates a male with scrotal testes or a female with one or more of the following: pregnant; perforate vagina; swollen nipples, open pubic symphysis.

males had scrotal testes, and one female had a perforate vagina and possibly was pregnant (Table 1).

Radiotelemetry.—Each animal captured in 1991 was implanted with a radiotransmitter, and with one exception, each was released within 48 h of capture. The first muskrat released (NO in Table 1) probably died of trauma related to the operation and was found only 5 m from the house near which she had been trapped. Only three muskrats were tracked ≥1 week and were located enough times to enable us to arrive at reasonable estimates of home range (Table 1).

Compared to muskrats ME and CU, the much greater size of home range and number of houses occupied by muskrat LD (Table 1; Fig. 4a) was not a function of time under observation, as LD covered nearly the length of his home range twice within a 24-h period on several occasions and occupied three houses within one 2.5-h period. No other muskrat was seen or trapped within the vicinity of these five mats, although the possibility of a mate or even another male with overlapping home range is not precluded, especially because LD was not known to use four of the active houses on the five mats.

Muskrats ME and CU were relatively sedentary and were found on two occasions in the same house (Fig. 4b), which contradicts Birkenholtz's (1963, 1972) assumption that *N. alleni* is strictly solitary. Both muskrats also used another house, but not at the same time.

Radiotelemetry also provided some insights into predation pressure on the population. Three round-tailed muskrats released with radiotransmitters appeared to have been predated (Table 1), two by alligators *(Alligator mississippiensis)* and one by a raptor, probably a barred owl

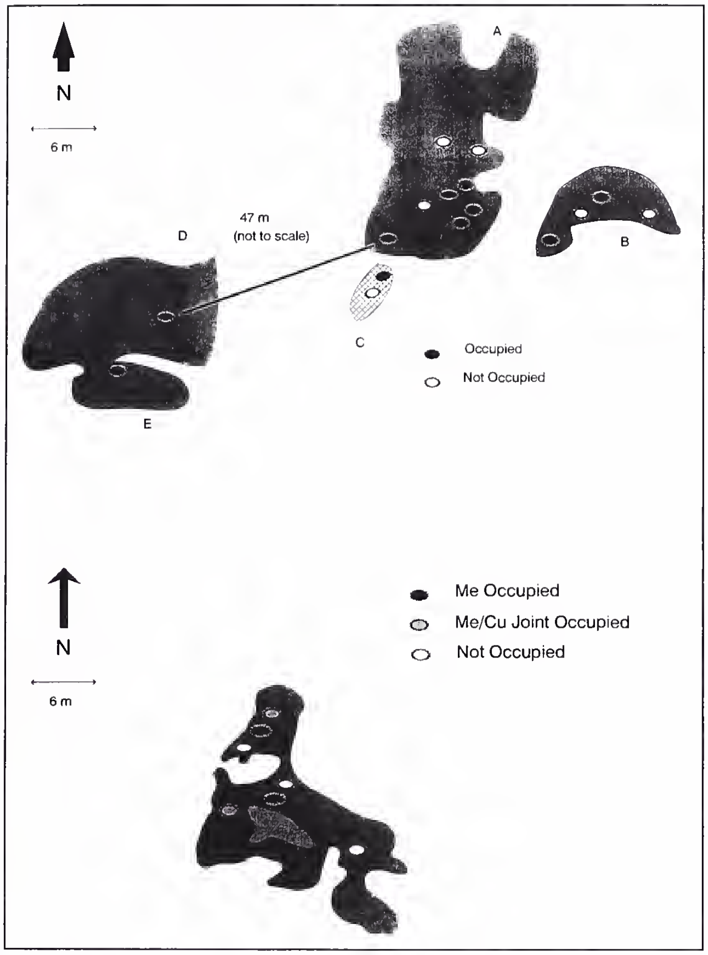

Fig. 4.—A, top half: Diagram of five mats (A-E) used by round-tailed muskrat LD over 55 days of observation, including all 14 houses appearing on mats and indication of the 10 houses that radiotelemetry revealed he was occupying. B, bottom half: Diagram of round-tailed muskrats CU and ME over 7 days of observation, including all seven houses appearing on mats and indication of the four houses that radiotelemetry revealed one or both were occupying.

(Strix varia). CU's radiotransmitter was found in shallow water at the base of a whitewashed snag where an owl had been spotted previously. In 1988 at Grand Bay, we observed a red-shouldered hawk *(Buteo lineatus)* flying away, clutching a round-tailed muskrat in its talons. The three apparent cases of predation occurred within 1 week of release of muskrats with radiotransmitters. Radiosignals of two other muskrats, which may have been predated, were lost within 1 and 2 days, respectively, of release (Table 1).

DISCUSSION

We found, as have other studies, that, even in suitable habitat, houses of *N. alleni* were tightly clumped into colonies, perhaps because of limited availability of mats in the appropriate successional stage (Birkenholz, 1963; Lefebvre, 1982; Steffen, 1978). Houses and mats were occupied for ≤3 years in our study, compared to 5 months reported by Birkenholz (1963). Our study, the first to present movement and home-range data from radiotelemetry, suggests that the estimate of 2.2 houses/ animal (Birkenholz, 1963) may be low, given that one of our animals occupied 10 houses. Our radiotelemetry data indicate remarkably small home ranges for *N. alleni* compared to mammals of similar body size (Table 1; Swihart et al., 1988), and sharing of houses by two males suggests *N. alleni* may not be entirely solitary. Predation of *N. alleni* by alligators had not been documented prior to our study (Birkenholz, 1963; Porter, 1953).

Population densities, as assessed by counts of houses at Grand Bay, were as much as one or two orders of magnitude lower than those from central Florida (Birkenholz, 1963), and long-term population dynamics suggest a 2-year cycle (Fig. 3), which may be a response to the cyclical succession of formation and die-back of the floating-mat habitat.

Although population densities are low, distribution of *N. alleni* appears fairly continuous within suitable habitat from north-central Florida into south-central Georgia. Although not documented previously in the latter area, populations probably have existed here since pre-settlement times. Subspecific affinities of these populations are not known, but the new localities in Lowndes and Brooks counties are closer to the previously described range of N. a. apalachicolae in northern Florida than to the range of N. a. exoristus, known from the eastern Okefenokee Swamp in Georgia (Hall, 1981; Schwartz, 1953). There is an apparent 80-km gap in distribution between populations at Grand Bay and Okefenokee Swamp, although suitable habitat is present in this area.

Perceived distributional gaps at this northern limit of distribution may result from a combination of the fragmented, isolated distribution of palustrine wetlands and the generally low population densities causing localized extinction. Birkenholtz (1963) documented dispersal of *N. alleni* across roads and other upland habitats and via ditches from populations south of Gainesville, Florida. The degree of isolation of habitat also may have been lesser and availability of dispersal corridors greater farther south. With ecological densities of 1-3 muskrats/ha, a litter size of 2.2 (low for an arvicoline—Birkenholtz, 1963), and high rates of predation we witnessed in the population in Grand Bay, the species may not sustain a viable population so far from its center of abundance where suitable habitat is so isolated. This seems a more plausible explanation for the northern distributional limit than the direct effects of cooler climate (Birkenholtz, 1972).

Populations of *N. alleni* in Georgia may be the most peripheral sinks for species dispersal and, therefore, may be recolonized only following periods of exceptionally high densities in more central populations. However, natural dispersal is an unlikely event given continuing fragmentation and destruction of wetland habitats in the Southeast (Mitsch and Gosselink, 1993). This may explain why two colonies observed previously in southwestern Georgia were not found in our recent aerial surveys. A viable population may survive in the 30,000 ha of wet prairies and islands of Okefenokee Swamp. Harper (1927) estimated the population at 10,000, but Porter (1953) and recent visits (T. Hon) found few signs of active houses.

Another potential problem for viability of populations is interruption of the natural hydroperiod and suppression of natural fires. During droughts, summer burns historically consumed much of the shrubby and hardwood growth that encroached on the marsh and burned accumulated peat to considerable depths, restoring a deeper-water system conducive to the cyclical succession of the round-tailed muskrat's floating-mat habitat. Winter droughts also occasionally exposed roots of aquatic macrophytes to a killing frost, causing die-backs of such plants as *Nymphaea, Pontederia,* and *Sagittaria,* and yielding organic matter for production of mats in the future. Loss of habitat through hydrarch succession may be a problem throughout the range of the round-tailed muskrat and may explain why Porter (1953) found *N. alleni* to be either extirpated or rare in many areas of Florida that previously had supported dense populations.

Densities also may react negatively to introduced fire ants (Harper, 1927; Johnson, 1961; Porter, 1953; Steffen, 1978). We found many abandoned muskrat houses taken over by colonies of fire ants, and other colonies of muskrats often were close to fire-ant mounds. Infestations of fire ants may negatively affect survival of nestlings. As succession proceeds toward a dense, shrub bog community, fire ants may become more abundant and may serve as an additional link between anthropogenic fire exclusion or water management and decline in populations of *N. alleni.*

A rapid, cyclical succession of the mat community can occur, based on our observations at Grand Bay. After an open-water area with floating macrophytes or low emergents experiences a die-off due to winter drought, drawdown, or treatment with herbicides, the partially decayed mass of vegetation floats up to the surface as a mat of peat or muck. The new mat becomes colonized by *Lachnanthes* and *Carex,* followed by a second wave of plant colonists, including *Dulichium, Eleocharis, Hypericum, Xyris, Bidens,* and *Decodon.* This densely vegetated mat yields dominance to *Woodwardia,* and eventually to woody shrubs such as *Lyonia* and *Itea*, and trees such as *Nyssa* and *Taxodium.* At this stage, mats usually attain coalescence and anchor to woody plants rooted in the substrate, and vertical filling of the wetland begins. Preferred food plants of *N. alleni* are crowded out and escape routes severely limited. A natural agent of retrogression in this system is the greater sandhill crane *(Grus canadensis tabida),* which winters on Grand Bay wetlands. We saw cranes dig up and eat fleshy roots of plants such as *Lachnanthes* and in the process quickly denude mats. Cranes may carry seeds of earlier seral species on their feet or feathers or in their feces, further prolonging earlier successional states more amenable to *N. alleni.*

The majority of marsh habitat at Grand Bay, itself, and in the 5,200-ha Grand Bay wetlands complex is not currently in suitable condition for long-term viability of populations of *N. alleni.* Much of it has succeeded rapidly in recent years due to low water levels and fire exclusion. One side benefit to the herbicide treatment of water lilies was proliferation of new mats, which quickly were colonized and led to a relatively dramatic increase in population from one year following a 4-year low. We hope to incorporate management of mats as a new tool in providing additional habitat. Mats could be moved into new positions, anchored, and seeded, or planted with sedges, redroot, or species of grasses (e.g., *Panicum hemitomum*) providing fleshy roots or leaves suitable for construction of houses (Birkenholtz, 1963; Porter, 1953). A recent successful introduction of the non-migratory Florida sandhill crane *(G. c. pratensis)* to the Grand Bay wetlands should further enhance survival and reproduction of *N. alleni* by promoting early mat-successional phases and emergent marsh. High densities of *N. alleni* sometimes reported for populations in Florida may never be attained, but through prescribed burning, water-level management, management of mats, and restoration of sandhill cranes, habitat available to the round-tailed muskrat may be increased and the prospects for its long-term survival in Georgia enhanced.

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POPULATION DYNAMICS OF THE BEACH MOUSE (*PEROMYSCUS POLIONOTUS TRISSYLLEPSIS*): A SIMULATION STUDY

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A computer simulation model was developed to test predictions relating to changes in size and structure of panmictic and spatially subdivided populations under different demographic and environmental assumptions. The model was evaluated using data obtained from the population of endangered beach mice (*Peromyscus polionotus trissyllepsis*) at Gulf Islands National Seashore, Florida. Simulations were carried out for both panmictic and subdivided populations. In all cases considered, panmictic populations survived longer. Observed decreases in persistence times of subdivided populations were functions of the underlying assumptions of the model (e.g., demography, spatial distributions, and occurrence of extinction and recolonization events). The study emphasized the need for more extensive behavioral and life-history data for simulation purposes. It also identified certain critical demographic factors needed to decrease the level of uncertainty associated with model predictions.

Substantial recent work in conservation biology has focused on the process of extinction and factors required for the persistence of species (Shaffer, 1981). While desirable (Hartl and Clark, 1989), in most field experiments, it usually is impossible to study the interactive effects of multiple demographic variables (life span, dispersal, mean litter size, mean number of litters per year, survival) on the dynamics of a population. Therefore, many biologists use computer-simulation algorithms to predict effects of these variables on genetic and demographic structure of populations. This approach may provide new insights into the effects of conservation practices (Lacy, 1987).

We attempted to model the effects of altering ecological variables on temporal and spatial structure of a population of endangered beach mouse, *Peromyscus polionotus trissyllepsis*, using a simulation program. The long-term goal for this model is to aid in determining future actions necessary for conservation. By predicting effects that different conservation strategies might have on extinction probabilities in populations of mice, this model may provide insight into the consequences of various management decisions.

Conservation biologists recognize the potential significance of population structure in preservation of rare and endangered species (Chesser, 1991; Haig et al., 1990; McCauley, 1991). Many factors, such as total amount of available habitat, its distribution, and extent of population subdivision, affect the extinction probability of a resident species (Forney and Gilpin, 1989). As habitats disappear or become fragmented, populations often are reduced to small, isolated breeding units. These isolated units or subpopulations may be more susceptible to the effects of genetic drift than a single large population (Lacy, 1987). Furthermore, the biotic and abiotic landscape within a subpopulation may exist as either continuous or as spatially patchy units (Slatkin, 1987). These two extremes of population structure can have different genetic and demographic consequences (McCauley, 1991).

Many mathematical models describe consequences of population structure (e.g., Slatkin, 1987; Wright, 1931). Genetic consequences of these models have been given increasing attention (McCauley, 1991). Much of the current theory of population structure contrasts the impact of finite population size with consequences of movement (gene flow) among populations. Subsequently, the role of dispersal in population divergence and in management approaches is the subject of intense debate among conservationists (Primack and Miao, 1992; Simberloff and Cox, 1987). However, other factors such as founder events, effective population sizes, patterns of migration, breeding tactics, and rates of genotypic and phenotypic change (e.g., Chesser, 1991; Lewontin, 1974; Wright, 1951) also govern structure and stability of natural systems. Patterns of local extinctions and recolonization also may have significant consequences for subdivided populations (McCauley, 1991).

Conservation biology suffers because effects of dispersal and geographic structuring in natural populations are poorly understood (Slatkin, 1987). Most population models attempt to predict patterns of change under assumptions of population structure and migration that often are too broad to allow specific recommendations regarding management of a given threatened or endangered species. In fact, different models may provide conflicting messages to population managers.

We developed a general simulation model to identify and test predictions relating to long-term trends and changes in population size, structure, and gene frequencies of populations. The proposed model attempts to examine interactive effects of multiple variables (initial population size, resource quality and availability, dispersal ability, litter size, mean number of litters per year, age to maturity, monthly survival of litters to subadult stage, and monthly survival of subadults to adults) that influence long-term changes in a population. Ultimately, the model may test predictions of alternate management strategies for conservation of the Perdido Key beach mouse, one of four subspecies of the old-field mouse *(P. polionotus)* formally listed as endangered (Rave and Holler, 1992).

We compared and contrasted two different models of population structure, a continuous panmictic model and a discrete population model, to examine effects of variables listed above on the extinction probabilities of the Perdido Key beach mouse. The panmictic model treated the population as a single unit, whereas the discrete model was based on actual distribution of the population at Gulf Islands National Seashore, Florida. Using sensitivity analysis, we attempted to identify those variables for which additional information from the population of beach mice at Gulf Islands National Seashore was critical. We report our efforts to evaluate effects of varying parameters for life span, litter size, and survivorship on the demographic structure of populations generated by both models.

POPULATION MODELED

Empirical data used in this study were obtained from beach-dwelling populations of the old-field mouse, *P. polionotus.* Beach mice represent isolated or semi-isolated populations that occupy coastal dune systems in Alabama and Florida. Populations of old-field mice occurring along the coast of Alabama and the panhandle of Florida were described as separate subspecies (Hall, 1981). These taxonomic designations were based on morphological differences that may reflect levels of evolutionary divergence among these populations (Bowen, 1968). Although controversial, these taxonomic groupings generally are supported by recent genetic investigations (T. H. Pitzer and M. C. Wooten, pers. comm.).

All subspecies along the Gulf Coast currently are protected under state or federal laws. The subspecies selected as the model for our study, the Perdido Key beach mouse *P. p. trissyllepsis,* is protected as endangered by both federal and state governments (United States Fish and Wildlife Service, 1985). In April 1986, the Perdido Key beach mouse existed as a single population of ca. 30 individuals in Alabama (Holler et al., 1989). Because habitat available for the mice was restricted, loss of genetic diversity and the potential for stochastic loss of the population during a normal population low were major concerns. To alleviate the imminent threat of extinction faced by this population, a second population was established at Gulf Islands National Seashore, Florida, through translocation (Holler et al., 1989). The initial population at Gulf Islands National Seashore was established with 15 pairs of mice from Gulf State Park, Alabama, November 1986-April 1988 (Holler et al., 1989). Three pairs were moved in the initial translocation; additional pairs were translocated as the population in Alabama recovered. The mice have been monitored since that time and data from live-trapping surveys indicated that the population probably exceeded 100 individuals by early 1990 (Holler and Rave, 1991). To provide for genetic diversity and gene flow, exchanges of individuals between populations at Perdido Key and Gulf Islands National Seashore have continued.

The re-established population on Gulf Islands National Seashore has occupied up to ca. 11 km of coastal dunes. This habitat is located at the eastern terminus of Perdido Key on a narrow strip that is bounded by Gulf waters to the south and Perdido Bay to the north. A trapping transect was established starting at the east end of the dune habitat and extending 7 km west. Trapping data were available for this 7-km transect and simulation studies were designed to model this portion of the habitat. Henceforth, this transect is referred to as the study area.

METHODS

Simulation model.—A computer simulation model was developed to identify and test predictions of long-term changes in demographic structure of populations. The simulation routine was developed in the C-programming language for use with IBM PC compatibles. Program logic, development criteria, and validation results are available in Sankaran (1993).

Two models of population structure were considered; a continuous panmictic model and a discrete population model. All simulations conducted for both models estimated demographic structure of the population at 1-month intervals. We varied initial population size, survival rate, gestation period, age to maturity, and dispersal ability. Both models incorporated overlapping generations, sessile adults, and monogamy. These assumptions are consistent with the biology of this species.

Continuous model.—The first model considered a continuous panmictic population structure. This continuum model assumed a lack of geographic subdivision and the entire population was treated as a single panmictic unit. For all simulations, mice were assumed to be continuously distributed across the study area and there were no limits to distance an individual was capable of dispersing. Although no natural populations are truly panmictic (Pianka, 1974), small population subunits may essentially be panmictic. An understanding of how these subunits function is required to understand dynamics of populations as a whole.

Because *P. polionotus* is primarily a monogamous species in which individuals tend to pair permanently (Blair, 1951; Foltz, 1981), the model was modified to accommodate the effects of monogamy. Rather than every individual having an equal probability of mating with every other individual of opposite sex, every unpaired individual had an equal probability of pairing with every other unpaired individual. Once paired, individuals remained so until death of a partner.

Discrete population model.—Models of discrete population structure define populations in which distribution of individuals across the geographic range of a species is patchy or clumped. One of the first such models was the island model defined by Wright (1931), which represents an infinite collection of equivalent subpopulations, each receiving immigrants at a rate *m*, chosen at random from other subpopulations. This model was later modified to represent a finite number of subpopulations (*n*), each equally capable of sending and receiving individuals from every other (Latter, 1973). In both of these models, there are no geographic restrictions on gene flow and they represent the extreme in long-distance gene flow (Slatkin, 1985). The stepping-stone model, introduced by Kimura (1953), represents the extreme in short-distance gene flow. In this model, subpopulations are located in a regular one-, two- or three-dimensional lattice. Gene flow occurs between a population and its immediate neighbors, with each subpopulation exchanging the same fraction of individuals with its neighbors.

Most models are simplistic. All natural populations are geographically bounded and patterns of migration and gene flow observed in nature rarely display simple regularity. We examined effects of geographic subdivision of a population using a model that went one step further in trying to mimic natural populations when compared to earlier models. Our model was a modification of the stepping-stone model because migration did not necessarily occur only between a subpopulation and its immediate neighbors, and the fraction of individuals migrating between subpopulations was not always the same.

Simulations carried out for the discrete population model were similar to ones conducted for the continuous panmictic model, but the population was subdivided. For these simulations, a lattice was used to represent geographic range of the mice. To simulate geographic subdivision, the study area initially was subdivided into units called resident areas, each capable of supporting a

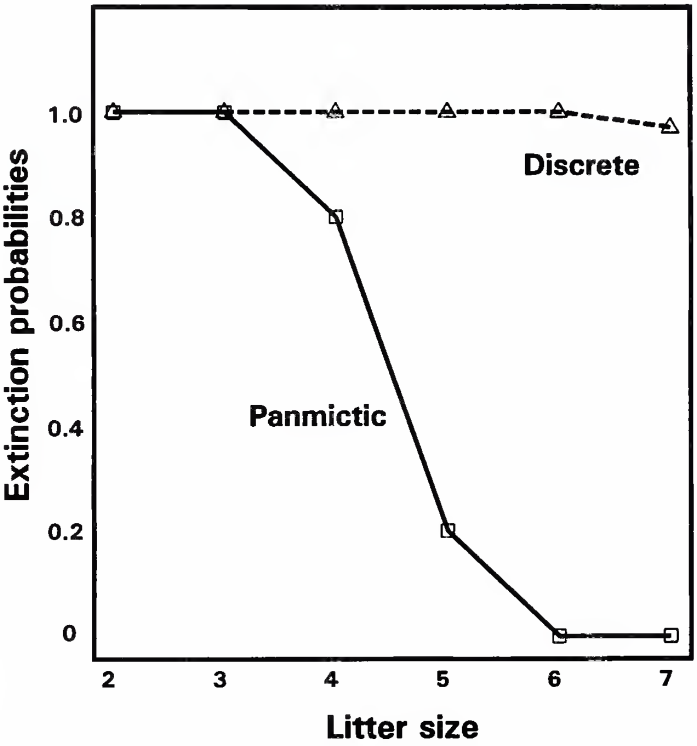

Fig. 1.—Mean probabilities of extinction for populations of *Peromyscus polionotus trissyllepsis* for differing fixed litter sizes derived from panmictic and discrete models. Data points represent the mean of 30 replicate simulations.

subpopulation. Each resident area, defined as average dispersal distance of adult mice, was 124.35 m long (calculated by averaging seasonal dispersal distances of adults—Hill, 1989), resulting in a total of 56 resident areas across the study area. Linear habitat occupied by mice was represented using a 56 by 1 lattice, where each cell in the lattice was a potential resident area of a subpopulation (Fig. 1). Cells in the lattice were not necessarily identical with respect to factors such as carrying capacity, occupation, and quality and availability of resources. To determine carrying capacity of each resident area, estimates of quality and availability of resources were taken at intervals of 125 m across the length of the actual study area. Resident areas were graded on a scale of 1 to 5 with carrying capacities of 20, 30, 40, 50, and 60, respectively. Actual capture data was used to determine number of mice in each resident area. Individuals were clustered into subpopulations where they were trapped most frequently and represented on the lattice for the simulations. Because simulations were carried out using empirical population estimates, individuals for which actual trapping data were not available were randomly assigned resident areas.

Dispersal occurs chiefly while animals are young and before they have established ranges as adults (Burt, 1940; Dice and Howard, 1951; Howard 1949, 1960). Once home sites have been established by adults, monogamous *Peromyscus,* in particular, rarely leave them (Davenport, 1964; Ribble, 1992). Average dispersal distance of subadults is much greater than average dispersal distance of adults (Hill, 1989; Smith, 1968). Consequently, in all simulations with the discrete population model, juveniles were capable of migrating, but adults were not. This restriction on dispersal of adults may be greater than that occurring in natural populations; it provides a contrast to the panmictic model, where there were no restrictions on movements.

Each subpopulation occupying a cell in the lattice was treated as a panmictic unit. Adults were randomly paired with other adults that occupied the same resident area. Skewed sex ratios resulted in some individuals remaining unpaired. Once paired, individuals were allowed to mate and produce offspring after a gestation period of 1 month (Table 1). This model differed from the panmictic model in that individuals were not capable of migrating across the entire length of the study area. Because size of resident area was assumed to be the mean dispersal distance of adults, adults moved only within resident areas.

Migration occurred at maturity when a subadult was ready to leave the natal site and establish a home site of its own. Distance migrated by an individual was defined by sampling from a normal distribution of observed dispersal distances in beach mice (Hill, 1989). The final destination of a migrant was a function of dispersal distance and a randomly selected direction of migration. Number of individuals migrating to and from a particular resident area was a function of number of offspring produced and carrying capacity of the resident area. If a resident area was already at its carrying capacity, all individuals migrating to that area were removed from the simulation. Once at a destination, individuals randomly paired with any available partner and produced offspring.

Initial simulation parameters.—Numerical increase and persistence of any population are affected by factors such as initial population size, litter size, number of

Table 1.—*Listing of demographic variables and sources for* Peromyscus polionotus.

Variable	Value	Source
Life span	6 months-2 years	N. R. Holler (pers. comm.)
Gestation period	24-31 days	Layne (1968)
Mean litter size	4.09 ± 1.33	N. R. Holler (pers. comm.)
Mean litters/year	range, 1-5	
Age at maturity	6-7 weeks	Blair (1951)
Monthly survival rate	0.680	Rave and Holler (1992)

litters per year, and survival rate. As a result, knowledge of individual effects of these factors is vital to understanding their combined effects. To examine these potential interactions, initial parameter settings for all simulations were based on actual capture data. Population estimates were generated with CAPTURE (Otis et al., 1978) using live-trapping data from July 1988 (N. R. Holler and J. E. Moyers, in litt.). This analysis resulted in an initial population estimate of 69 animals (31 males and 38 females).

To determine effect of maximum lifespan, simulations were run for both models, except that survivorship was held constant at 0.68 and maximum lifespans were varied at 12, 18, and 24 months. Simulations using both models were conducted with an initial population size of 69 (31 males and 38) with a constant monthly survival rate of 0.68 and mean litter size of 4.09 ± 1.33.

Litter sizes were estimated from captive-colony data (N. R. Holler, pers. comm.). The average used for most simulations was 4.09 ± 1.33 (Table 1) with extremes of one to eight. However, to determine effect of varying litter size, simulations using fixed litter sizes of 2, 3, 4, 5, 6, and 7 also were run.

To determine effect of survivorship, multiple simulations were conducted for varying survival rates with fixed litter sizes of four and five offspring and with the actual estimate of 4.09 ± 1.33 offspring and with an initial population of 69 individuals. To determine survival rate required to maintain a stable population, simulations were carried out with both models using different monthly survival rates on a trial-and-error basis. Monthly survival rates of 0.25, 0.50, 0.65, 0.68, 0.69-0.80 (0.01 increments), and 0.85 were examined. Simulations were carried out for different litter sizes to analyze combined effects of these two variables on dynamics of the population.

Each simulation was carried out for a period of 5 (60 time intervals), with 30 replicates for each run. Time intervals were preset at 1 month because it was the minimum period between any two events, either mating to birth or birth to maturity. Survival was checked by generating a random number between 0 and 1 and comparing it with the specified survival rate. If the random number was greater than the specified survival rate, the individual was removed from the simulation. If one of the partners of a pair died, the living individual was allowed to pair with any unpaired individual. If the male partner of a pair died after it had mated, the female was not allowed to re-pair until after it had given birth and offspring were weaned.

RESULTS

Effect of varying life span.—For the panmictic model, mean time to extinction of the population increased with increasing life span. Increasing the life span of the mice from 12 to 18 months increased average persistence time of the population from 36.7 to 40.4 months, and increasing the life span from 18 to 24 months increased persistence from 40.4 to 42.5 months. These differences were not significant ($F = 2.23$; $P = 0.11$). These results were consistent with the fact that in the simulations, and in nature, few mice actually survived for 18 months.

For the discrete model all of the hypothetical populations went extinct before the end of the 5-year simulation period. As with the panmictic model, mean time to extinction increased with increasing life span. Increasing life span from 12 to 18 months had a greater, but non-significant, effect on mean times to extinction and fixation than did an increase in life span from 18 to 24 months (20.5, 22.4, and 22.8, respectively), but with significantly lower overall averages compared to the panmictic model ($F = 223.12$; $P < 0.001$).

Effect of varying litter size.—Using the panmictic model, the probability of extinction of the population decreased as litter size increased to a value of five fixed offspring (Fig. 1). The probability of extinction over a 5-year period decreased from 0.8 for a fixed litter size of 4.0 offspring to 0.2 for a litter size of 5.0 (Table 2). If the assumed mean litter size for the population is 4.09 ± 1.33 (Table 1), a four-fold increase in survival chances of the population is predicted if every female produced one more offspring than usual. For litter sizes of 6.0 and 7.0, extinction probabilities fell to zero, with none of the 30 replicates going extinct before the end of the 5-year simulation period. The mean time to extinction also increased as litter size increased with the shortest value observed for fixed litter sizes of two (Table 2).

Using the discrete model, all replicates went extinct before the 5-year simulation period ended, except for those with a fixed litter size of 7.0 offspring (Fig. 1). In this case, all populations but one went extinct during the 5-year period. Mean times to extinction increased as litter size increased, but did not surpass 60 months (Table 2). Both linear and exponential regressions yielded significant goodness of fit (linear: $r^2 = 0.989$, $P < 0.001$;

Table 2.—*Probability of extinction and mean time to extinction (in months) for populations of* Peromyscus polionotus trissyllepsis *with different fixed litter sizes using a monthly survival rate of 0.680.*

	Probability of extinction		Mean time to extinction	
Litter size	Panmictic	Discrete	Panmictic	Discrete
2	1.00	1.00	22.06	18.43
3	1.00	1.00	29.57	19.80
4	0.80	1.00	38.00	22.43
5	0.20	1.00	46.67	25.96
6	0.00	1.00	60+	28.60
7	0.00	0.97	60+	31.40

exponential: $r^2 = 0.993$, $P < 0.001$). Although a greater proportion of observed variance was accounted for by exponential regression, it was not possible to conclude that the observed correlation between litter size and mean time to extinction was exponential and not linear.

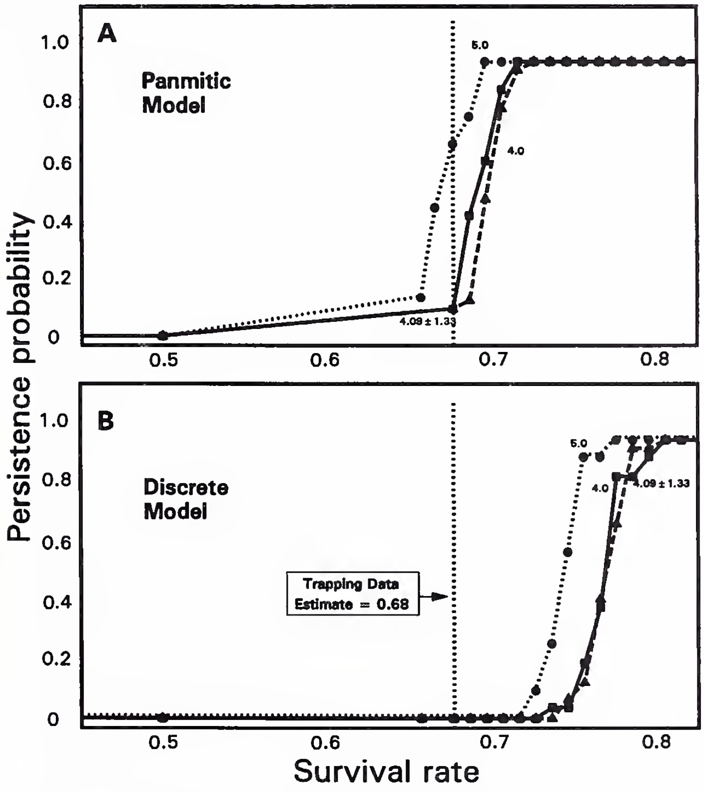

Fig. 2.—Persistence probabilities for populations of *Peromyscus polionotus trissyllepsis* for different monthly survival rates for fixed litter sizes of 4.0 and 5.0 offspring and a normally distributed litter size with a mean of 4.09 ± 1.33 for panmictic (A) and discrete (B) models.

Effect of varying survivorship.—At survival rates of 0.25 and 0.5, all replicates for both models went extinct before 60 months (Figs. 2A and 2B). However, an increase from the reported monthly survival rate of 0.68 to a survival rate of 0.71, resulted in an increase in persistence probability for the panmictic model from 0.1 to 0.9 (Fig. 2A). For a monthly survival rate of 0.72 or greater, all replicates survived the entire simulation period. For fixed litter sizes of 4.0 and 5.0 offspring, similar patterns of change were observed in persistence probabilities with increasing survival rates (Fig. 2A). As litter size increased, lower survival rates were required to maintain a stable population. For a litter size of 4.0 offspring, a monthly survival rate of 0.73 was required, whereas for a litter size of 5.0 offspring, survival rate needed to maintain a stable population fell to 0.7. Mean persistence times also were correlated to survival rate and increased exponentially as survival rate increased (normally distributed litter size: $r^2 = 0.952$, $P < 0.001$; litter size = 4.0: $r^2 = 0.942$, $P < 0.001$; litter size = 5.0: $r^2 = 0.949$, $P < 0.001$; Fig. 2A).

Different monthly survival rates also affected simulations with the discrete population model. For monthly survival rates of ≤ 0.73, all replicates went extinct before 60 months (Fig. 2B). Increasing survival rate from 0.74 to 0.81 increased survival chances. For a litter size of 4.09 ± 1.33 offspring, a monthly survival rate of 0.81 was required for the population to survive the entire 5-year simulation period (Fig. 2B). For fixed litter sizes of 4.0 offspring, a monthly survival rate of 0.81 also was required if the population was to survive for 5 years. For a fixed litter size of 5.0 offspring, lower monthly survival rates enabled the population to persist longer. In this case, a survival rate of 0.78 increased the chance of the population surviving the simulation period to 100%. Similar patterns were observed for different litter sizes as survival rate increased (Fig. 2B). As litter sizes increased, population stability was achieved with lower survival rates. Mean time to extinction also was significantly correlated to survival rate. The correlations between monthly survival rates and mean time to extinction were exponential (litter size = 4.0: $r^2 = 0.935$, $P < 0.001$; litter size = 4.09 ± 1.33: $r^2 = 0.9542$, $P < 0.001$; litter size = 5.0: $r^2 = 0.945$, $P < 0.001$).

DISCUSSION

Prediction of population extinctions is one of the fundamental challenges of conservation biology (Gilpin and Soulè, 1986). If extinction probabilities can be predicted for a population under different environmental and demographic conditions, management programs may be tailored to maximize survival of a species.

We developed a computer simulation model that predicted changes in size and structure of panmictic and spatially subdivided populations under different demographic and ecologic conditions. It also identified certain factors needed to enhance future models. The goal of our study was not to prescribe an optimal population size and structure for the population of mice, but to define effects that different conservation strategies might have on extinction probability of *P. p. trissyllepsis*.

Extinction events may be classified as either deterministic or stochastic (Gilpin and Soulè, 1986). Deterministic extinctions result from removal of something essential, such as space, shelter, or food (e.g., habitat loss). Stochastic extinctions, conversely, are those that result from normal random changes in the environment or demography of a species.

Stochastic extinctions also can be differentiated into two types; those that occur due to demographic stochasticity and those that result from environmental stochasticity (Gilpin and Soulè, 1986). Demographic stochasticity results from chance variation in mating, birth, and death, and is independent for each individual. Environmental stochasticity results from random changes in the environment that are external to the population. These changes include year-to-year fluctuations in environmental conditions, as well as catastrophic events (Caughley and Gunn, 1996).

The panmictic population model developed in this study was a demographic stochastic model, whereas the discrete population model incorporated effects of both demographic and environmental stochasticity. Demographic stochasticity was simulated by random changes in individual survival, life span, and litter size. Variation in quality of habitat and carrying capacities provided the environmental stochastic component. Environmental stochasticity was modeled only on a spatial (difference in quality and carrying capacities of different resident areas) and not a temporal scale (seasonal changes in habitat quality, carrying capacity, etc.). Consequently, populations were subject only to effects of demographic stochasticity because all simulations were carried out under the same set of temporally stable environmental conditions.

If extinction is caused by demographic stochasticity alone, mathematical models predict that persistence of a population in a subdivided habitat be much lower than in a single large patch of the same total area (Quinn and Hastings, 1987; Wright and Hubbell, 1983). These predictions were reflected in the outcome of our simulations. Panmictic populations had lower extinction probabilities than subdivided populations. Persistence times also were greater for panmictic populations than subdivided populations of the same size. Unlike previous models based on birth and death rates, population growth in these simulations was based on a normally distributed litter size and a fixed monthly survival rate. The simulations also permitted overlapping generations. Furthermore, in the discrete population model, the spatial component of environmental stochasticity might have affected population dynamics even in the presence of temporal stability.

In the absence of deterministic extinction events, such as habitat destruction or human intervention, survival of a population is a function of birth rate and death rate. To ensure a stable population, effects of these two variables would have to be balanced. If these two factors do not cancel out, the population will not be stable, and will increase or decrease toward extinction.

Previous studies have predicted threshold values at critical population sizes of ca. 50 individuals (Frankel, 1974; Gilpin and Soulè, 1986; Shaffer, 1981; Shaffer and Samson, 1985; Soulè, 1980) based on the assumption that average birth rate exceeds average death rate by up to several times. Quinn et al. (1989) stated that if these conditions were met, a critical population size of just 20 individuals would be sufficient to offset extinction. Comparing these results with those of these simulations, one explanation for the high extinction probabilities observed is that a monthly survival rate of 0.68 and a mean litter size of 4.09 ± 1.33 are not adequate to maintain a stable population, taking into consideration the underlying model assumptions.

For a panmictic population with a mean reproductive output of 4.09 ± 1.33 offspring, a monthly survival rate of ca. 0.72 is required to achieve a persistence probability of 1.0 or ensure survival for a 5-year period. For subdivided populations under the same demographic conditions, a monthly survival rate of ca. 0.81 is required to ensure persistence over a 5-year period. Lower or higher monthly rates may be required depending on distribution of individuals. Increasing monthly survival rates also resulted in an increase in mean times to extinction. For both panmictic and subdivided populations, the observed increase in mean time to extinction was exponential.

Another demographic parameter that affected persistence probabilities was mean number of offspring per litter. For a panmictic population with a monthly survival rate of 0.68, an increase in litter size from 4.0 to 5.0 offspring resulted in a four-fold increase in persistence probability. A mean litter size of just over 5.0 offspring would be required to maintain a stable panmictic population. Conversely, litter size did not seem to be a major factor in discrete subpopulations. For the case of a subdivided population of 69 individuals, even fixed litter sizes as large as 7.0 offspring resulted in a persistence probability of only 0.03.

Increasing reproductive output also resulted in an increase in mean time to extinction of the population. In the panmictic model, the observed increase was linear. However, for the case in which the population was subdivided, it was not possible to conclude whether the increase was linear or exponential, as the regression analysis for both cases yielded significant results.

Panmictic populations were less prone to near-future extinction events than subdivided populations of the same size. However, in the presence of environmental stochasticity, mathematical models predict that moderately subdivided populations are likely to persist longer than either a highly subdivided population or a single contiguous population occupying the same area (Quinn and Hastings, 1987; Quinn et al., 1989). Hence, it would not be a good conservation strategy to conclude that a single large population is better suited to persist than subdivided populations until the model can be upgraded to investigate effects of both spatial and temporal environmental stochasticity.

Subdivision does not necessarily reduce persistence times as drastically as indicated by the model. The most probable reasons for high extinction rates observed in the case of subdivided populations are constraints associated with the model. Dispersal was a random process based on observed dispersal distances in beach mice and a randomly chosen direction of migration. Once an individual migrated to a particular resident area it was incapable of dispersing any further. Only juveniles were capable of dispersing across resident areas. Once an individual dispersed to a particular resident area, it remained there irrespective of quality of habitat, carrying capacity, or availability of potential mates. Furthermore, individuals were capable of mating only with individuals in the same resident area. These assumptions reduced the effective population size when number of individuals was low or if occupied resident areas were far apart. As a result, subdivided populations were more prone to extinction than panmictic populations. Contrast provided by the two models indicates the importance of obtaining field data on actual dispersal distances by both adult and subadult mice.

This population appeared to be vulnerable to extinction, even in simulations with the panmictic model, which was not constrained, when reported values were used for survival rate and litter size. This is consistent with our trapping results. The population began a large decline in spring 1992, and by autumn 1993, only 11 individuals were captured (N. R. Holler and J. E. Moyers, in litt.). This decline occurred despite continued translocation of mice to the population. Although a recovery began in winter 1994, we believe that the population could easily have become extinct.

All extinction probabilities were calculated based on the fraction of replicates that went extinct within the 5-year simulation period, and are valid only for that period. An extinction probability of zero for a 5-year time period does not ensure a stable population, but it implies that the probability of the population going extinct within the 5-year period is relatively low. Mean times to extinction were calculated based only on those replicates that went extinct before the end of 5 years, and hence, do not give any information about replicates that survived. Both of these indices are useful only within the realms of their applicability, which in this case was a period of 5 years.

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