

BAT COMMUNITY STRUCTURE, FORAGING ACTIVITY, AND EVENING BAT ROOST
SITE SELECTION IN LOBLOLLY PINE AND LONGLEAF PINE FORESTS OF GEORGIA

by

ADAM CARL MILES

(Under the Direction of Steven Castleberry)

ABSTRACT

During summers 2002 and 2003, I used mist nets, bat detectors, and radio-telemetry to investigate bat community structure, activity, and the day-roost selection of evening bats (*Nycticeius humeralis*) on mature longleaf and managed loblolly study sites in southwestern Georgia. The Seminole bat (*Lasiurus seminolus*), red bat (*L. borealis*), and evening bat were captured most frequently on each site. Bat activity was greater in mature pine than other habitats on the longleaf site, and activity was lesser in the hardwood habitat type on the managed site. Evening bats on the longleaf pine landscape selected roosts based on tree, plot, and landscape scale characteristics, while bats on the managed landscape selected roosts based on only the tree and plot characteristics. I hypothesized that the greater availability of roosting structures (abundant large trees and snags) on the longleaf site allowed evening bats to select roost sites that had more favorable landscape characteristics (i.e. closer to water and foraging sites).

INDEX WORDS: Anabat, bat activity, bat community, bat detector, evening bat, habitat use, *Nycticeius humeralis*, radiotelemetry, roost selection, Southeast

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

Bats comprise about one-sixth of mammalian species in the southeastern United States, but relatively little is known about their community structure and habitat use in the region (Brown 1997). Many species of bats use forests to meet at least one component of their life history requirements (Miller et al. 2003). Of the 18 species of bats found in the Southeast, nine use forests as their primary roosting and foraging sites (Carter 1998). Bat community structure and habitat use of pine (*Pinus* spp.) forests in the Southeast has not been adequately studied (Miller et al. 2003). Specifically, few studies have examined forest bat assemblages in mature longleaf pine (*Pinus palustris*) forests or intensively managed loblolly pine (*Pinus taeda*) plantations.

The longleaf pine forest ecosystem has been described as one of the most endangered forest ecosystems in the world (Outcalt and Sheffield 1996, Brockaway and Lewis 1997). Longleaf pine forests once dominated the Coastal Plain of the Southeast, covering as much as 37 million hectares, but currently have been reduced to less than 1.2 million hectares (Landers et al. 1995). Longleaf forests likely provided abundant habitat for a variety of bat species. The frequent fire interval associated with this ecosystem created sparse, open-canopy forests which were likely excellent foraging habitat. Large trees and lightning strike snags were abundant

throughout the landscape, providing cavity and bark roosting species with roosting structures. Conversely, to meet demands for forest products, the area covered by managed pine plantations in the South is expected to increase 67% from 12 million hectares in 1999 to 20 million hectares in 2040 (Wear and Greis 2002). The increasing intensity of management of these forests results in shorter rotations, loss of late successional forests, and declines in species diversity of vegetation communities (Allen et al. 1996). Conservation of biodiversity in both the remaining longleaf pine forests and intensively managed pine forests in the Southeast is critical.

Because bats spend over half of their lives in roosts, understanding roosting ecology is critical for their conservation (Fenton 1998). Roosts are important as sites for resting, pup-rearing, protection from weather, and information transfer (Kunz 1982, Wilkinson 1992). The evening bat (*Nycticeius humeralis*) is common in forested ecosystems across the Southeast (Barber and Davis 1969), and represents a model species for use in examining the influence of intensive timber management on bat roosting ecology. Despite the evening bat being a common species, there is only limited information on its roosting ecology. Evening bats have been known to use roosts such as Spanish moss (*Tillandsia usneoides*; Jennings 1958), exfoliating bark of snags (Jennings 1958, Chapman and Chapman 1990, Menzel et al. 1999, 2001), tree cavities (Rudolph et al. 1990, Menzel et al. 1999, 2001), and buildings (Chapman and Chapman 1990, Wilkinson 1992). However, roost site selection at multiple spatial scales in intensively managed forests and more natural pine forests remains uninvestigated.

Mist net and bat detector surveys are commonly employed to examine bat community structure (Murray et al. 1999, O'Farrell and Gannon 1999). Furthermore, bat detectors may be useful for examining the relative activity of foraging bats in relation to different forest management practices (Furlonger et al. 1987, Grindal and Brigham 1999). Although these types

of data is available for bats in the northwestern and northeastern United States, only limited information is available on the foraging activity of bats in the Southeast (Carter 1998, Owen 2000, Menzel et al. 2002).

Given the lack of information on bat community structure and roost site selection in pine forests of the Southeast, the objectives of this research were to: (1) examine the roost site selection of evening bats in relation to forest management, and (2) describe bat community structure and compare the relative activity of foraging bats among habitat types within intensively managed loblolly and mature longleaf pine landscapes.

This thesis is written in manuscript format, with Chapters 2 and 3 prepared for submission to scientific journals. Chapter 1 is an introduction to the study and literature review. Chapter 2 is a multi-scale investigation of evening bat roosting ecology and will be submitted to the *Journal of Wildlife Management*. Chapter 3 describes bat community structure and activity and will be submitted to *Southeastern Naturalist*. Chapter 4 summarizes important findings and conclusions.

LITERATURE REVIEW

Roost Site Selection

Because of the importance of roost sites to bats (Kunz 1982) and the hypothesis that lack of suitable roost sites may limit bat populations (Humphrey 1975), roost studies traditionally have been important components of bat research. It was not until the late 1980's with the advent of radio transmitters small enough to be placed on forest bats, that researchers could consistently identify tree roosts used by forest bats. However, this research has largely focused on a few species of bats in the western and mid-western United States (Miller et al. 2003). Roosting ecology studies usually have shown that forest bats use larger than average snags in the

intermediate stages of decay as roosts (Ormsbee and McComb 1998, Rabe et al. 1998, Weller and Zabel 2001). However, most of these studies have limited inferential scope, because they only investigated characteristics at the small spatial scale (i.e. roost tree), had small sample sizes, or only investigated roost selection in a single forest condition.

Although bat species range over a variety of forest conditions, previous roost selection studies have typically been conducted within one forest type (Ormsbee and McComb 1998, Weller and Zabel 2001) or around a limited number of capture locations (Betts 1998). Data derived from studies in one forest condition can not be expected to accurately represent roost selection by the same species in other forest types (Miller et al. 2003). For example, the western long-eared myotis (*Myotis evotis*) selected large snags when capture locations were surrounded by mature forest, and stumps when capture locations were surrounded by intensively managed forests (Waldien et al. 2000). Had inference been drawn to the species with one of the forest conditions eliminated from the study, conclusions would have been spurious.

Two studies have used radio transmitters to study evening bat roost site selection in forested environments in the Southeast. Menzel et al. (1999) identified roosts used by evening bats on Sapelo Island, Georgia. They found that evening bats used predominately loblolly and slash (*Pinus elliottii*) pine tree cavities and exfoliating bark as roosts. However, only limited inference can be drawn from these data, because of a sample size of only 3 bats and 14 roosts. Menzel et al. (2000, 2001) determined that evening bats on the Savannah River Site in South Carolina roosted under exfoliating bark or in cavities of living or dead trees in open, mature longleaf pine stands or hardwoods within beaver (*Castor canadensis*) ponds. They suggested that intensively managed pine forests with nearly complete canopy cover may not provide adequate roost structures for this species. However, during 1998-2000 evening bats were the

second most commonly captured species (20% of captures) on an intensively managed loblolly pine forest in Mississippi, suggesting that roost structures were available in this landscape (Miller 2003).

Previous studies on evening bat roosting ecology only addressed roost site selection at a local scale, comparing identified roost structure characteristics to randomly selected trees within the same stand (Menzel et al. 1999, 2000, 2001). With these data, roost selection can only be described at the stand level. With evening bats, as with many forest bat species, landscape-level roost selection may have an important role in managed forests, but has not been investigated.

Bat Community Structure and Activity

Mist net surveys are commonly employed to examine bat community structure throughout North America (Murray et al. 1999, O'Farrell and Gannon 1999). The direct capture of individuals allows positive species identification, reproductive assessment, and estimation of sex and age ratios (Murray et al. 1999, Miller 2003). Previous surveys in the Southeast indicate that the bat community is dominated by a few common species (Seminole [*Lasiurus seminolus*], red [*L. borealis*], and evening bats; Humphrey 1975, Carter 1998, Miller 2003). Capture records also have been reported in different forest types including hardwood dominated (Owen 2000), mature longleaf pine (Carter 1998), and intensively managed (Miller 2003) landscapes throughout the region. However, capture efforts have not included multiple landscapes with different forest management objectives.

Bat detectors have become a useful tool for the study of bats because of ease of use, reduced labor through passive recording options, and the ability to study bats without direct disturbance. Because multiple bat detectors can be placed in the field to record simultaneously, they have been used to examine the relative activity of foraging bats in relation to different forest

management practices (Furlonger et al. 1987, Grindal and Brigham 1999, Owen 2000, Menzel et al. 2002). Studies have demonstrated the importance of old growth or mature forests (Crampton and Barclay 1998, Humes et al. 1999), edge (Menzel et al. 2002), and open (Menzel et al. 2002, Erickson and West 2003) habitats to bats. Habitat associations have been linked to foraging strategies and morphological characteristics of bat species or guilds (Patriquin and Barclay 2003). Acoustic detections of aerial foraging (aerial hawking) species are greater in open and edge habitats where quick flight can be used to capture prey (Patriquin and Barclay 2003). Cluttered habitats are avoided by aerial hawking species, but are regularly used by species that capture insects off the surface of vegetation (gleaners; Patriquin and Barclay 2003)

Bat detector surveys and activity studies are constrained by important assumptions and limitations (Sherwin et al. 2000). Large spatial and temporal variation in bat activity has been noted with bat detectors (Hayes 1997, Sherwin et al. 2000, Weller and Zabel 2002). Weller and Zabel (2002) found that up to 70% more passes were detected at a single location within a forest depending on orientation of bat detectors toward an opening. This variation can be reduced by controlling the height, angle, and orientation of the detector toward an opening within sampled habitats. Hayes (1997) noted temporal variation in activity throughout the night, summer, and year and recommended simultaneously sampling all habitats of interest to control for variation. In order to compare activity between habitat types, Sherwin et al. (2000) suggested that equal detection probabilities between habitat types during each sampling period must also be assumed. Britzke (2003) found that detection probabilities between open and cluttered habitat types were not equal because of differing areas of space sampled by detectors.

The majority of acoustic detection studies have been conducted in the western United States and Canada (Thomas 1988, Crampton and Barclay 1998, Grindal and Brigham 1998,

Humes et al. 1999, Seidman and Zabel 2001). The impacts of forest management practices on the diverse bat fauna of the west likely differs from the relatively simple community in the Southeast. The few studies that have investigated habitat use with bat detectors in the Southeast have focused on the effects of harvest methods on bat activity (Owen 2000, Menzel et al. 2002). The activity of bats within habitat types associated with mature longleaf and intensively managed loblolly landscapes has not been addressed. Information on bat activity within intensively managed pine plantations in the Coastal Plain of the southeastern United States is needed for development of management strategies for the region that address wildlife habitat and biodiversity concerns.

LITERATURE CITED

- Allen, A. W., Y. K. Bernal, and R. J. Moulton. 1996. Pine plantations and wildlife in the Southeastern United States: an assessment of impacts and opportunities. U.S. Department of the Interior, Information and Technology Report. National Biological Service, Washington, D.C., USA.
- Betts, B. J. 1998. Roosts used by maternity colonies of silver-haired bats in northeastern Oregon. *Journal of Mammalogy* 79:643-650.
- Britzke, E. R. 2003. Use of ultrasonic detectors for acoustic identification and study of bat ecology in the eastern United States. Dissertation, Tennessee Technological University, Cookeville, USA.
- Brockaway, D. G., and C. E. Lewis. 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. *Forest Ecology and Management* 96:167-183.

- Brown, L. N. 1997. A guide to the mammals of the southeastern United States. University of Tennessee Press, Knoxville, USA.
- Carter, T. C. 1998. The foraging ecology of three species of bats at the Savannah River Site, South Carolina. Thesis, University of Georgia, Athens, USA.
- Chapman, S. S., and B. R. Chapman. 1990. Bats from the coastal region of southern Texas. *Texas Journal of Science* 42:13-22.
- Crampton, L. H., and R. M. R. Barclay. 1998. Selection of roosting and foraging habitat by bats in different-aged aspen mixedwood stands. *Conservation Biology* 12:1347-1358.
- Erickson, J. L., and S. D. West. 2003. Associations of bats with local structure and landscape features of forested stands in western Oregon and Washington. *Biological Conservation* 109:95-102.
- Fenton, M. B. 1998. Science and the conservation of bats. *Journal of Mammalogy* 78:1-14.
- Findley, J. S. 1976. The structure of bat communities. *The American Naturalist* 110:129-139.
- Furlonger, C. L., H. J. Dewar, and M. B. Fenton. 1987. Habitat use by foraging insectivorous bats. *Canadian Journal of Zoology* 65:284-288.
- Grindal, S. D., and R. M. Brigham. 1998. Short-term effects of small-scale habitat disturbance on activity by insectivorous bats. *Journal of Wildlife Management* 62:996-1003.
- Grindal, S. D., and R. M. Brigham. 1999. Impacts of forest harvesting on habitat use by foraging insectivorous bats at different spatial scales. *Ecoscience* 6:25-34.
- Hayes, J. P. 1997. Temporal variation in activity of bats and the design of echolocation-monitoring studies. *Journal of Mammalogy* 78:514-524.
- Humes, M. L., J. P. Hayes, and M. W. Collopy. 1999. Bat activity in thinned, unthinned, and old-growth forests in western Oregon. *Journal of Wildlife Management* 62:553-561.

- Humphrey, S. R. 1975. Nursery roosts and community diversity of Nearctic bats. *Journal of Mammalogy* 56:321-346.
- Jennings, W. L. 1958. The ecological distribution of bats in Florida. Dissertation, University of Florida, Gainesville, USA.
- Kunz, T. H. 1982. Roosting ecology of bats. Pages 1-55 in T. H. Kunz, editor. *Ecology of bats*. Plenum Press, New York, USA.
- Landers, J. L., D. H. Van Lear, and W. D. Boyer. 1995. The longleaf pine forests of the Southeast: requiem or renaissance. *Journal of Forestry* 93:39-44.
- Menzel, M. A., D. M. Krishon, T. C. Carter, and J. Laerm. 1999. Notes on tree roost characteristics of the northern yellow bat (*Lasiurus intermedius*), the Seminole bat (*L. seminolus*), the evening bat (*Nycticeius humeralis*), and the eastern pipistrelle (*Pipistrellus subflavus*). *Florida Scientist* 62:185-193.
- Menzel, M. A., T. C. Carter, W. M. Ford, and B. R. Chapman, and J. Ozier. 2000. Summer roost tree selection by eastern red, Seminole, and evening bats in the upper Coastal Plain of South Carolina. *Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies* 54:304-313.
- Menzel, M. A., T. C. Carter, W. M. Ford, and B. R. Chapman. 2001. Tree roost characteristics of subadult and female adult evening bats (*Nycticeius humeralis*) in the upper coastal plain of South Carolina. *American Midland Naturalist* 145:112-119.
- Menzel, M. A., T. C. Carter, J.M. Menzel, W. M. Ford, and B. R. Chapman. 2002. Effects of group selection silviculture in bottomland hardwoods on the spatial activity patterns of bats. *Forest Ecology and Management* 162:209-218.

- Miller, D. A. 2003. Species diversity, reproduction, and sex ratios of bats in managed pine forest landscapes of Mississippi. *Southeastern Naturalist* 2:59-72.
- Miller, D. A, E. B. Arnett, and M. J. Lacki. 2003. Habitat management for forest bats of North America: a critical review of habitat studies. *Wildlife Society Bulletin* 31:30-44.
- Murray, K. L., E. R. Britzke, B. M. Hadley, and L. W. Robbins. 1999. Surveying bat communities: a comparison between mist nets and the Anabat II bat detector system. *Acta Chiropterologica* 1:105-112.
- O'Farrell, M. J., and W. L. Gannon. 1999. A comparison of acoustic versus capture techniques for the inventory of bats. *Journal of Mammalogy* 80:24-30.
- Ormsbee, P. C., and W. C. McComb. 1998. Selection of day roosts by female long-legged myotis in the central Oregon Cascade Range. *Journal of Wildlife Management* 62:596-603.
- Outcalt, K. W. and R. M. Sheffield. 1996. The longleaf pine forest: trends and current conditions. *USDA Forest Service Research Bulletin SRS-9*.
- Owen, S. F. 2000. Impacts of timber harvest in the central Appalachians hardwood region on bat foraging and roosting behavior. Thesis, University of Georgia, Athens, Georgia, USA.
- Patriquin, K. J., and R. M. R. Barclay. 2003. Foraging by bats in cleared, thinned, and unharvested boreal forest. *Journal of Applied Ecology* 40:646-657.
- Rabe, M. J., T. E. Morrell, H. Green, J. C. DeVos, Jr., and C. R. Miller. 1998. Characteristics of ponderosa pine snag roosts used by reproductive bats in northern Arizona. *Journal of Wildlife Management* 62:612-621.
- Rudolph, D. C., R. N. Conner, and J. Turner. 1990. Competition of red-cockaded woodpecker roosts and nest cavities: effects of resin age and entrance diameter. *Wilson Bulletin* 102:23-36.

- Seidman, V. M., and C. J. Zabel. 2001. Bat activity along intermittent streams in northwest California. *Journal of Mammalogy* 82:738-747.
- Sherwin, R. E., W. L. Gannon, and S. Haymond. 2000. The efficacy of acoustic techniques to infer differential use of habitat by bats. *Acta Chiropterologica* 2:145-153.
- Thomas, D. W. 1988. The distribution of bats in different ages of Douglas-fir forests. *Journal of Wildlife Management* 52:619-626.
- Waldien, D. L., J. P. Hayes, and E. B. Arnett. 2000. Day-roosts of female long-eared myotis in western Oregon. *Journal of Wildlife Management* 63:785-796.
- Wear, D.N., and J.G. Greis. 2002. The southern forest resource assessment: Summer, Report. United States Department of Agriculture, Forest Service, General Technical Report SRS-54.
- Weller, T. J., and C. J. Zabel. 2001. Characteristics of fringed myotis day roosts in northern California. *Journal of Wildlife Management* 65:489-497.
- Wilkinson, G. S. 1992. Information transfer at evening bat colonies. *Animal Behavior* 44:501-518.

CHAPTER 2

EVENING BAT ROOST SITE SELECTION IN LONGLEAF AND LOBLOLLY PINE
DOMINATED LANDSCAPES IN SOUTHWEST GEORGIA¹

¹ Miles, A.C., S. B. Castleberry, D. A. Miller, and L.M Conner. To be submitted to The Journal of Wildlife Management.

ABSTRACT

Natural longleaf pine forests have been drastically reduced while intensively managed loblolly pine (*Pinus taeda*) plantations have increased in the Southeast. Intensively managed pine plantations have short rotation times (< 30 years) which may limit development of large trees and snags, and therefore could limit opportunities for cavity and bark roosting bats. During summers 2002 and 2003, we used radio-telemetry to investigate the day-roost selection of evening bats (*Nycticeius humeralis*) on mature longleaf (natural) and intensively managed loblolly pine (managed) sites in the Gulf Coastal Plain of Georgia. We used Akaike's Information Criterion (AIC) to investigate differences in multi-scale roost selection at both sites. We tracked 99 evening bats to 168 individual roost trees. Bats roosted in a variety of structures, but live conifers (*Pinus* spp. and *Taxodium distichum*) were the most common type of tree used on both study areas. Evening bats were more abundant, formed larger maternity colonies, roosted closer to their capture pond, and used more roosts on the natural site than on the managed site. Evening bats on the natural site selected roosts based on tree, plot, and landscape scale characteristics, while bats on the managed site selected roosts based on only the tree and plot scale. We hypothesize that the greater availability of roosting structures (abundant large trees and snags) on the natural site allowed evening bats to select roost sites that had more favorable landscape characteristics (i.e. closer to water and foraging sites). This study demonstrates the importance of evaluating bat roost selection in landscapes with different management objectives and habitat conditions.

INTRODUCTION

Bats comprise about one-sixth of mammalian diversity in the southeastern United States, but relatively little is known about their community structure and habitat use in the region

(Brown 1997). Many species of bats use forests to meet at least one component of their life history requirements (Miller et al. 2003). Of the 18 species of bats found in the Southeast, nine use forests as their primary roosting and foraging sites (Carter 1998). Bat habitat use of pine (*Pinus* spp.) forests in the Southeast has not been adequately studied (Miller et al. 2003). Specifically, few studies have examined forest bat roosting ecology in mature longleaf pine (*Pinus palustris*) forests or intensively managed loblolly pine (*Pinus taeda*) plantations.

The longleaf pine forest ecosystem has been described as one of the most endangered forest ecosystem in the world (Outcalt and Sheffield 1996, Brockaway and Lewis 1997). Longleaf pine forests once dominated as much as 37 million hectares in the Southeast, but currently have been reduced to less than 1.2 million hectares (Landers et al. 1995). These forests likely provided abundant habitat for cavity and bark roosting bats because large trees and lightning strike snags were abundant throughout the landscape. Conversely, to meet demands for forest products, the area covered by managed pine plantations in the Southeast is expected to increase 67% from 12 million hectares in 1999 to 20 million hectares in 2040 (Wear and Greis 2002). The intensity of management of these forests results in shorter rotations, loss of late successional forests, and may result in declines in species diversity of vegetation communities (Allen et al. 1996). Intensive management limits development of large trees and snags, and therefore could limit opportunities for cavity and bark roosting bats. Roosts are important as sites for resting, pup-rearing, protection from weather, and information transfer (Kunz 1982, Wilkinson 1992). Because bats spend over half of their lives in roosts, understanding roosting ecology is critical for conservation (Fenton 1998).

The evening bat (*Nycticeius humeralis*) is common in forested ecosystems across the Southeast (Barber and Davis 1969) and represents a model species for examining the influence

of intensive forest management on bat roosting ecology. Despite being common, there is limited information on evening bat roosting ecology. Evening bats have been known to use Spanish moss (*Tillandsia usneoides*; Jennings 1958), exfoliating bark of snags (Jennings 1958, Chapman and Chapman 1990, Menzel et al. 1999, 2001), tree cavities (Menzel et al. 1999, 2001), and buildings (Chapman and Chapman 1990, Wilkinson 1992) as roosts. However, roost site selection at multiple spatial scales and among differing landscape management regimes remains uninvestigated.

Previous research has focused on the importance of small scale characteristics on the roost site selection of forest bats (Ormsbee and McComb 1998, Weller and Zabel 2001). Landscape scale characteristics also likely influence roost selection. Our approach was to incorporate small scale and landscape scale characteristics into a single study to examine which spatial scales were most important to roost site selection of evening bats within intensively-managed loblolly and mature longleaf pine landscapes. Specifically, we were interested in determining if evening bats selected roost sites differently based on spatial scales among the 2 landscapes with different management intensities, types, and objectives.

STUDY AREA

We conducted the study in the Upper Coastal Plain physiographic region of southwestern Georgia, between 31°50' and 31°4' N latitude and 84°40' and 83°39' W longitude. This region is characterized by hot, humid summers with average daily temperatures of 27° C. Afternoon thunderstorms occurred frequently in summer and average annual precipitation was 132 cm/year.

We selected two sites for study, one that represented the historic longleaf condition and one that represented an intensively managed pine landscape (Figure 2.1). The Joseph W. Jones Ecological Research Center at Ichauway (natural site), in Baker County, Georgia was a 12,000-

ha research site managed with biennial prescribed fire to simulate natural disturbance patterns and promote a landscape similar to the historic longleaf pine ecosystem. Longleaf forests were between 70 to 90 years old, with individual trees >300 years old scattered throughout the site. Southern red oak (*Quercus falcata*), sweetgum (*Liquidambar styraciflua*), and other hardwoods commonly occurred individually within mature pine forests. Snags (especially pine, to a lesser extent hardwoods) were also common in forested areas. Riparian hardwood forests, mixed pine/hardwood forests, and wildlife openings were scattered throughout the site.

The Aultman Tract (managed site), in Worth County, Georgia, approximately 70 km to the northwest of Ichauway, was a 14,000-ha area consisting primarily of loblolly pine plantations managed by Weyerhaeuser Company for sawtimber on a 30-year rotation. Typical management for pine stands included site preparation and planting, vegetation management, commercial thinning, pruning, and fertilization. This management resulted in even-aged stands of different successional stages distributed in a mosaic throughout the landscape. A dense hardwood midstory of sweetgum, persimmon (*Diospyros virginiana*), and oaks often were present in stands between 20 to 30 years old. Interspersed throughout the site were non-plantation habitats >50 years old including streamside management zones, mature pine-hardwood and hardwood forests.

METHODS

Capture and Radiotelemetry

We captured evening bats from late May to early-September 2002 and 2003 with 6 to 18 m x 2.4 m mist nets set over ponds, small streams, and roadside ditches surrounded by a variety of habitats throughout each study site. We recorded mass (g), forearm length (mm), sex, age (Anthony 1988), and reproductive condition (Racey 1988) of captured bats. We attached 0.43-g, 0.45-g (Micro-Pip, Biotrack, Wareham, Dorset, UK) and 0.52-g (LB-2, Holohill Systems Ltd.,

Carp, Ontario, Canada) radio transmitters to the fur-clipped inter-scapular region of evening bats with Skin Bond® (Pfizer Hospital Prod. Group, Inc., Largo, Florida, USA) surgical cement. Bats were held for 20 minutes to allow adhesive to set and released at point of capture. Transmitter mass was 2.5 – 6.1% of the bat as recommended by Aldridge and Brigham (1988) and within the transmitter/body mass ratio range of similar studies (Ormsbee and McComb 1998, Waldien et al. 2000, Weller and Zabel 2001). All radio-tagged bats appeared to fly normally after release.

We used TRX-2000S (Wildlife Materials International, Inc., Murphysboro, Illinois, USA), R-1000 (Communications Specialists, Inc., Orange, California, USA), and R-2000 (Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA) receivers and 4- and 6-element yagi antennas to track bats to day-roost structures. Beginning the day after capture, bats were tracked daily or as time permitted, until either the transmitter failed or was recovered. To assess variability in roost selection among evening bat populations on each site, we focused our efforts on tracking a larger number of bats and prioritized daily tracking to new bats or those with fewer roosts. Our approach may have resulted in fewer roost structures per bat, but allowed us to draw inferences based on a larger sample of individual bats, which may be preferable to earlier studies (Miller et al. 2003). We conducted dusk emergence counts on a sample of roosts to either confirm bat use of structures that were difficult to identify with telemetry, or to count the number of exiting bats. Location of day-roost structures were recorded using a Pathfinder Pro XR (Trimble Navigation Limited, Sunnyvale, California, USA) Global Positioning System (GPS) with differential correction and imported into a geographic information system (GIS, ArcInfo, Environmental Systems Research Institute, Redlands, California, USA).

Because our objective was to determine if evening bats selected roosts differently based on roost availability throughout each landscape, we compared roosts to randomly selected trees within each study area. We used GIS to generate random points and selected the nearest overstory tree (>9.5 cm diameter at breast height [dbh]) as a random tree. This approach differed from previous studies for two main reasons (Ormsbee and McComb 1998, Menzel et al. 2000, Waldien et al. 2000). First, we defined the entire study area as available to radio-tagged bats because we actively trapped sites throughout each area and we were interested in roost selection by the population of evening bats throughout the landscape. Second, we defined any overstory tree, with or without visible cavities or signs of damage, as available to radio-tagged bats. Previous studies and our own data indicated that evening bats selected a wide variety of tree types and sizes as roosts, including healthy, live trees with no obvious signs of damage (Menzel et al. 1999, Menzel et al. 2001). Available trees were not used by radio-tagged bats during the study, but we could not be sure that they were not used by other bats (Bernardos et al. 2004).

Habitat Sampling

At each roost or random tree we recorded tree species, class (live or snag), dbh (cm), and height (m). In four quadrants around the roost or random tree, we measured the distance (m), species, live or snag, dbh (cm), and height (m) of the nearest overstory (>9.5 cm dbh) and midstory ($2 \text{ cm} < 9.5 \text{ cm}$) tree using the point-center-quarter method (Cottam and Curtis 1956, Conner and Godbois 2003). We used these data to calculate plot metrics (Table 2.1). We assumed that overstory trees >30 m and midstory trees >15 m from the roost tree would have little impact on bat roost selection, and designated these as maximum distances. Maximum distances were used in calculations when trees were missing from quadrants.

To calculate stand and landscape metrics, we used a GIS to divide each study area into four habitat types (mature pine, closed canopy pine, open, hardwood). Habitat definitions were simplified for consistency between sites. Mature pine included upland stands with a pine dominated canopy on the natural site and thinned pine stands (approx 13 to 30 years old) on the managed site. Closed pine stands were young, dense stands with almost complete canopy closure. Open habitat on the natural site included fields and wildlife food plots, and primarily clear cuts and regeneration stands <8 years old on the managed site. Hardwood included upland hardwood and mixed pine hardwood (hardwood dominated) stands, riparian areas, and cypress/forested wetlands on each site. Most hardwood areas on the managed site were designated as reserve areas and received limited management.

Stand variables described stand size and juxtaposition of the stand in relation to other habitat types and landscape features. Stand variables also included distance from the structure to water (stream, pond, or wetland), edge (or road), and each other habitat type (habitat in which the roost or random site resided was recorded as zero). We did not include stand age in multivariate analysis because pine stands on the natural site were similar in age. Landscape variables were calculated by creating a 430 m buffer around each roost and random tree and calculating the area of each habitat type (Table 2.1). We used a buffer size of 430 m because this was the average roost to roost distance for radio-tagged bats in the study, and represents a conservative estimate of the area which influenced roost site selection.

Analysis and Model Development

We developed 16 multivariate models to describe evening bat roost site selection on each study area. We pooled data across sex and age classes to determine which characteristics were most important to all evening bats at each site. We assigned variables to four spatial scale

categories (tree, plot, stand, landscape, Table 2.1). Models were all possible additive combinations of categories that described these spatial scales. We considered all models to have the potential for providing information on describing roost site selection. Because our study design and use of multiple-scale multivariate models differed from previous bat roosting studies, we considered our analysis to be exploratory.

We used logistic regression (Allison 2000) to create models, and used the second order Akaike's Information Criteria (AIC_c) to identify the most parsimonious model and predict variable importance (Burnham and Anderson 2002). We considered the model with the lowest AIC_c and all models $<2 \Delta_i$ as the best approximating models. We also calculated the Akaike weight (w_i) for each model, representing the probability of that model as being the best model in the set of candidate models (Burnham and Anderson 2002). We used model-averaged parameter estimates and unconditional standard errors to determine the importance of individual variables within the set of multivariate models with $>0.90 w_i$. We calculated odds ratios from averaged parameter estimates representing the increase in probability of a site being used as a roost by an evening bat for every unit increase in the predictor variable (Allison 2000).

RESULTS

We captured 144 evening bats during 83 nights (8514 net hours) of trapping at both sites. We averaged 1.2 ± 0.18 (mean \pm se) evening bats/hour on the natural site and 0.71 ± 0.15 evening bats/hour the managed site. We tracked 99 of 100 tagged evening bats to 169 individual roost trees. One bat (managed site) either left the study area or the radio failed and could not be located. Bats were located for 1 – 16 days (natural = 7.5 ± 0.5 , managed = 4.8 ± 0.5). On the natural site, we tracked 32 females to 55 trees, 19 males to 34 trees, and 9 juveniles to 22 trees ($n = 60$ bats to 111 trees). On the managed site, we tracked 18 females to 28 trees, 15 males to 22

trees, and 6 juveniles to 8 trees ($n = 39$ bats to 58 trees). Individual bats used 2.0 ± 0.14 roost trees on the natural site and 1.62 ± 0.15 roost trees on the managed site. Bats roosted an average of 1217 ± 145 m from the capture location on the managed site and 853 ± 58 m from the capture location on the natural site. Fourteen trees (natural = 9, managed = 5) were used by more than one radio tagged bat during the study, but were used only once in analysis. Adult males roosted alone, while females and juveniles roosted in groups or alone. We found 8 maternity colonies with over 100 bats (max = 490) and 11 colonies >30 bats on the natural site, and two colonies with 7 bats on the managed site.

Bats roosted under bark or in cavities of a variety of structures, but live conifers (*Pinus* spp. and *Taxodium distichum*) were the most common type of tree used on both study areas (natural = 57%, $n = 64$; managed = 60%, $n = 35$). On the natural site, 75% of roosts were in pines ($n = 83$), mostly longleaf ($n = 79$), and 25% hardwoods ($n = 28$), primarily oaks ($n = 27$). On the managed site, bats roosted in 39% loblolly pine ($n = 23$), 26% hardwood ($n=15$), and 32% bald cypress ($n = 19$). Sixty percent ($n = 14$) of the live loblolly pines used on the managed site were fork-topped trees that had a cavity at the base of the main fork. Because the cypress roosts occurred in streamside management zones and forested wetlands (hardwood habitat type), they were classed as hardwoods for the remainder of the analysis. Twenty-five percent of roosts on the natural ($n = 28$) and 26% of roosts on the managed site ($n = 15$) were snags. The mean height and dbh of trees used as roosts were 22 ± 0.5 m and 50 ± 1.8 cm on the natural site, and 15 ± 0.9 m and 26 ± 1.3 cm on the managed site (Table 2.2). Mature pine was the most common habitat type used by roosting evening bats on the natural site (78%, $n = 87$), while hardwood (48%, $n = 28$) and mature pine (31%, $n = 18$) were used most often on the managed site. Ten

roost trees (natural = 3, managed = 7) were located off the study sites and were not included in the multivariate analysis.

Roost Site Modeling

The model with the lowest AIC_c on the natural site was obtained using characteristics of the tree, plot, and landscape (Table 2.3). Two models that contained stand characteristics were $<2 \Delta_i$ and considered strongly competing. The w_i for the top model ($w_i = 0.402$) was only slightly greater than the next two closest models ($w_i = 0.365, 0.209$). The sum w_i of the top three models exceeded 0.90, indicating that there was a $>90\%$ chance that one of these models was the best approximating model of the 16 considered. These three models contained characteristics of the tree and plot, as well as higher level variables (buffer and/or stand).

The sum of Akaike weights (Σw_i) for all variables on the natural site were nontrivial (>0.50), but only 9 variables had model averaged confidence intervals that did not contain 0, indicating that they provided the most information about roost site selection (Figure 2.2; see Appendix A for parameter estimates and odds ratios). These included 2 tree variables (height, live or snag), 2 plot variables (mean overstory height, mean overstory distance), 2 stand variables (mature pine, water), and 3 buffer variables (open, hardwood, mature pine). These variables provided the most information about evening bat roost site selection on the natural site.

On the managed site, the model with the lowest AIC_c was obtained using only tree and plot characteristics (Table 2.4). This was the only model within $2 \Delta_i$ (next model = $7.5 \Delta_i$). The w_i for this model ($w_i = 0.959$) exceeded 0.95, indicating that there was $>95\%$ chance that this was the best approximating model of the 16 considered.

On the managed site, only variables describing the tree and plot had $\Sigma w_i > 0.1$ (tree and plot $\Sigma w_i > 0.99$), indicating that these were the most important variables. Five of these variables

(live or snag, mean overstory distance, distance to nearest overstory tree, mean midstory height, mean midstory distance) provided the most information about evening bat roost site selection on the managed site as indicated by confidence intervals that did not contain 0 .

DISCUSSION

Evening bats roosted under bark or in cavities of live or dead trees of a variety of species and sizes. They exhibited greater flexibility in roost structure selection than other species of cavity roosting bats (Betts 1998, Ormsbee and McComb 1998, Weller and Zabel 2001). Single roosting bats (both sexes) also frequently selected trees with little or no visible signs of damage from the ground, which differs from previous work on cavity roosting bats (Vonhof and Barclay 1996, Ormsbee and McComb 1998, Weller and Zabel 2001). Waldien et al. (2000) suggested that the use of multiple types of roosts by long-eared myotis (*Myotis evotis*) allowed individuals to adjust to availability of different types of structures throughout the landscape. Similarly, evening bat use of a variety of structures likely enables adjustment to landscapes with different availability of roosting structures. Even with the exhibited plasticity in roost selection, we observed differences in evening bat roost behavior and selection between natural longleaf and intensively managed loblolly pine landscapes.

Evening bats were more abundant, formed larger maternity colonies, roosted closer to their capture pond, and used more roosts on the natural site than on the managed site. These quantitative measures provide evidence that the natural site provided higher quality roosting habitat for evening bats. Although we did not quantify reproduction or recruitment, the greater abundance of large maternity colonies on the natural site may indicate greater reproductive output. While there were likely colonies that were not found on the managed site, our experience on the sites suggests that a real difference exists.

We actively trapped sites distributed throughout each landscape. The greater distance from the capture pond to roosts on the managed site may be related to a reduced availability of roost structures in the landscapes surrounding capture locations. There is likely an energetic cost associated with increased commuting distances from foraging and drinking locations to roost sites (Menzel et al. 2001). Additionally, evening bats on the natural site used more roosts than the managed site suggesting that multiple roosts were available within the area used by individual bats. Bats may benefit from the use multiple roosts in response to ectoparasite loads, microclimate, and disturbance (Lewis 1995).

The best multivariate models on each site contained tree and plot variables. The importance of characteristics of the tree and area around the tree (plot) in roost selection by evening and other bat species is well documented (Vonhof and Barclay 1996, Ormsbee and McComb 1998, Rabe et al. 1998, Menzel et al. 1999, 2001, Owen 2000). However, the top three multivariate models from the natural site also contained variables describing higher levels of selection. Evening bats on this site selected roosts based not only on tree and plot characteristics, but also on stand and landscape characteristics. Specifically, roost trees on the natural site were closer to the mature pine habitat and open water sources, and were surrounded by more open, hardwood, and mature habitat than randomly selected trees. Mature pine, open, and hardwood habitat types are preferred foraging locations for evening bats (Clem 1993, Carter 1998, Carter et al. 2004). We contend that the greater availability of roosting structures (abundant large trees and snags) throughout the landscape allowed evening bats to select roost sites that had more favorable landscape characteristics (i.e. closer to water and foraging sites), and therefore may provide benefits from reduced commuting costs. Evening bats on the managed site selected roost sites based on tree and plot characteristics. We suggest that favorable roosting sites were

more limited throughout the landscape and evening bats were unable to select roosts with favorable landscape characteristics.

Two variables (live tree or snag and mean overstory distance) describing the tree and plot were important regardless of the site. These variables suggest that snags within a forest stand were important roost sites to evening bats. Even though only 25% of roost structures on each site were snags, they were important because they were used in greater proportion to their abundance across the landscape. Large, lightning strike snags with thick sloughing bark in mature pine stands were important as maternal sites on the natural site where they were more abundant. Snags in mature pine stands on the managed site generally were small, with thin bark and were rarely used as roosts. The thin bark associated with these 20-30-year-old trees falls off quickly and may not provide favorable protection for roosting bats. Pine or hardwood snags in habitats that received little management (hardwood habitat type) were more frequently used on the managed site.

Five variables (dbh, mean overstory height, distance to nearest overstory tree, mean midstory height, mean midstory distance) within the tree and plot scales differed in importance between the landscapes, which likely reflects the different habitat conditions of each site. Similar to the results of Menzel et al. (2000), evening bats on the natural site selected roosts that were larger (dbh) and were surrounded by a shorter overstory canopy than randomly selected trees. The habitat on the natural site was likely similar to the habitat conditions on the Savannah River Site where the Menzel et al. (2000) study was conducted. Large trees may provide better and more permanent bark and cavities for roosting, be easier to locate and access, and provide more favorable thermoregulatory properties than smaller trees (Vonhof and Barclay 1996, Menzel et al. 2000). Evening bats on the managed site selected roosts that were farther from the

nearest overstory tree and had a shorter, more open midstory than random trees. Lower clutter around roost sites may reduce energy expenditure of flight and reduce the amount of time exposed to aerial predators (Vonhof and Barclay 1996, Betts 1998). The importance of clutter on the natural landscape was likely reduced because the 2-year fire rotation employed throughout this site creates open stands with an almost absent midstory. The difference in selection between the natural and managed landscapes suggests that evening bats select roost sites in the context of the habitat conditions of the site (Rabe et al. 1998, Waldien et al. 2000).

This study provides evidence that evening bat roosting behavior and roost site selection differs between natural longleaf landscapes and intensively managed landscapes. Because we lack proper replication at the landscape level, we cannot identify truly causal relationships regarding the differences between evening bat roosting behavior and roost site selection on the two landscapes examined. We hypothesize that the differences in evening bat roosting ecology between the sites were due to differences in availability of adequate roosting structures across the landscape. Replicated studies are needed to quantify landscape differences and identify causal mechanisms. Nonetheless, our study illustrated differences in bat roosting ecology among landscapes with different management objectives and further emphasizes the need for multi-scale studies (Miller et al. 2003).

MANAGEMENT IMPLICATIONS

While our models are useful for providing general insights into the selection of roost sites at multiple spatial scales, lack of landscape replication warrants using caution when making inferences regarding similar landscapes in the region based on our results. The 2-year prescribed fire prescriptions, the preservation of pine snags, and the mature nature of pine stands on the natural site likely created ideal roosting conditions for evening bats. We should not expect

industrial timberlands to provide the same quality of habitat for cavity roosting bats because management objectives dictate intensive management approaches that are not conducive to establishment or maintenance of snags or old trees. However, the presence of evening bats and identification of roost sites on the managed landscape indicate that suitable habitat conditions exist for bark and cavity roosting bats.

Given our data on the differences in roosting ecology at each of the study sites, we suggest management that increases roost structures across the landscape on intensively managed forests. For example, an added benefit of creating and preserving streamside management zones and hardwood reserve areas is that they may provide additional roost sites for evening bats. Many of these areas already receive protection or are not intensively managed due to difficult accessibility. Allowing maturation of hardwoods to promote cavity formation and senescence of pines to create snags would increase potential roosting habitat. Current best management practices (BMP's) for most southeastern states allow limited harvest (50-75% canopy removal) of trees in SMZ's and some forested wetlands (Georgia Forestry Commission 1999). Limited harvest of dense SMZ's may increase accessibility for evening bats by creating an open midstory, but care should be used to prevent removal of potential roost trees.

Large snags in the upland pine forests were important as maternity roosts on the natural site, but creating these types of structures on intensively managed forests is not a practical management option. Creating alternative structures in upland pine stands on managed forests should be explored. Fork-topped loblolly pines, which were the most frequently type of live pine used on the managed landscape, may provide an alternative to old trees and snags. Fork-topped loblolly pines are created when the terminal bud of a growing tree is damaged. Some fork-topped trees develop a cavity that forms between the two main forks of the tree, providing a

suitable roosting location for single bats or maternity colonies (A. C. Miles, University of Georgia, unpublished data). Fork-topped trees are considered undesirable and are typically removed during mid-rotation thinnings. Leaving fork-topped loblolly pines until final harvest of the stand would increase potential roosting habitat in upland pine stands.

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LITERATURE CITED

- Aldridge, H. D., and R. M. Brigham. 1988. Load carrying and maneuverability in an insectivorous bat: a test of the 5% "rule" of radio-telemetry. *Journal of Mammalogy* 69:379-382.
- Allen, A. W., Y. K. Bernal, and R. J. Moulton. 1996. Pine plantations and wildlife in the Southeastern United States: an assessment of impacts and opportunities. U.S. Department of Interior, Information and Technology Report. National Biological Service, Washington D.C., USA.
- Allison, P. D. 2000. Logistic regression using the SAS[®] system: theory and application. SAS Institute Inc., Cary, North Carolina, U.S.A.

- Anthony, E. L. P. 1988. Age determination in bats. Pages 47-55 in T. H. Kunz, editor. Ecology and behavioral methods for the study of bats. Smithsonian Institution Press, Washington, D.C., USA.
- Barber, R. W., and W. H. Davis. 1969. Bats of America. University Press of Kentucky, Lexington, USA.
- Bernardos, D. A., C. L. Chambers, and M. J. Rabe. 2004. Selection of gambel oak roosts by southwestern myotis in ponderosa pine-dominated forests, Northern Arizona. Journal of Wildlife Management 68:595-601.
- Betts, B. J. 1998. Roosts used by maternity colonies of silver-haired bats in northeastern Oregon. Journal of Mammalogy 79:643-650.
- Brockaway, D. G., and C. E. Lewis. 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. Forest Ecology and Management 96:167-183.
- Brown, L. N. 1997. A guide to the mammals of the southeastern United States. University of Tennessee Press, Knoxville, USA.
- Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.
- Carter, T. C. 1998. The foraging ecology of three species of bats at the Savannah River Site, South Carolina. Thesis, University of Georgia, Athens, USA.
- Carter, T. C, M. A. Menzel, B. R. Chapman, and K. V. Miller. 2004. Partitioning of food resources by synoptic eastern red (*Lasiurus borealis*), Seminole (*L. seminolus*) and evening (*Nycticeius humeralis*) bats. American Midland Naturalist 151:186-191.

- Chapman, S. S., and B. R. Chapman. 1990. Bats from the coastal region of southern Texas. *Texas Journal of Science* 42:13-22.
- Conner, L. M, and I. A. Godbois. 2003. Habitat associated with daytime refugia of fox squirrels in a longleaf pine forest. *American Midland Naturalist* 150:123-129.
- Cottam, G. and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37:451-460.
- Clem, P. D. 1993. Foraging patterns and the use of temporary roosts in female evening bat, *Nycticeius humeralis*, at an Indiana Maternity Colony. *Proceedings of the Indiana Academy of Science* 102:201-206.
- Fenton, M. B. 1998. Science and the conservation of bats. *Journal of Mammalogy* 78:1-14.
- Georgia Forestry Commission. 1999. Georgia's best management practices for forestry. Macon, Georgia, USA.
- Humphrey, S. R. 1975. Nursery roosts and community diversity of nearctic bats. *Journal of Mammalogy* 56:321-346.
- Jennings, W. L. 1958. The ecological distribution of bats in Florida. Dissertation, University of Florida, Gainesville, USA.
- Kunz, T. H. 1982. Roosting ecology of bats. Pages 1-55 in T. H. Kunz, editor. *Ecology of bats*. Plenum Press, New York, USA.
- Landers, J. L., D. H. Van Lear, and W. D. Boyer. 1995. The longleaf pine forests of the Southeast: requiem or renaissance. *Journal of Forestry* 93:39-44.
- Lewis, S. E. 1995. Roost fidelity of bats: a review. *Journal of Mammalogy* 76:481-496.

- Menzel, M. A., D. M. Krishon, T. C. Carter, and J. Laerm. 1999. Notes on tree roost characteristics of the northern yellow bat (*Lasiurus intermedius*), the Seminole bat (*L. seminolus*), the evening bat (*Nycticeius humeralis*), and the eastern pipistrelle (*Pipistrellus subflavus*). *Florida Scientist* 62:185-193.
- Menzel, M. A., T. C. Carter, W. M. Ford, and B. R. Chapman. , and J. Ozier. 2000. Summer roost tree selection by eastern red, Seminole, and evening bats in the upper Coastal Plain of South Carolina. *Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies* 54:304-313.
- Menzel, M. A., T. C. Carter, W. M. Ford, and B. R. Chapman. 2001. Tree roost characteristics of subadult and female adult evening bats (*Nycticeius humeralis*) in the upper coastal plain of South Carolina. *American Midland Naturalist* 145:112-119.
- Miller, D. A. 2003. Species diversity, reproduction, and sex ratios of bats in managed pine forest landscapes of Mississippi. *Southeastern Naturalist* 2:59-72.
- Miller, D. A, E. B. Arnett, and M. J. Lacki. 2003. Habitat management for forest bats of North America: a critical review of habitat studies. *Wildlife Society Bulletin* 31:30-44.
- Ormsbee, P. C., and W. C. McComb. 1998. Selection of day roosts by female long-legged myotis in the central Oregon Cascade Range. *Journal of Wildlife Management* 62:596-603.
- Outcalt, K. W. and R. M. Sheffield. 1996. The longleaf pine forest: trends and current conditions. *USDA Forest Service Research Bulletin SRS-9*.
- Owen, S. F. 2000. Impacts of timber harvest in the central Appalachians hardwood region on bat foraging and roosting behavior. Thesis, University of Georgia, Athens, USA.

- Rabe, M. J., T. E. Morrell, H. Green, J. C. DeVos, Jr., and C. R. Miller. 1998. Characteristics of ponderosa pine snag roosts used by reproductive bats in northern Arizona. *Journal of Wildlife Management* 62:612-621.
- Racey, P. A. 1988. Reproductive assessment in bats. Pages 31-43 *in* T. H. Kunz, editor. *Ecology and behavioral methods for the study of bats*. Smithsonian Institution Press, Washington, D. C., USA.
- Vonhof, M. J., and R. M. R. Barclay. 1996. Roost-site selection and roosting ecology of forest-dwelling bats in southern British Columbia. *Canadian Journal of Zoology* 74:1797-1805.
- Waldien, D. L., J. P. Hayes, and E. B. Arnett. 2000. Day-roosts of female long-eared myotis in western Oregon. *Journal of Wildlife Management* 63:785-796.
- Wear, D. N., and J. G. Greis. 2002. The southern forest resource assessment: Summer, Report. U. S. Department of Agriculture, Forest Service, General Technical Report SRS-54.
- Weller, T. J., and C. J. Zabel. 2001. Characteristics of fringed myotis day roosts in northern California. *Journal of Wildlife Management* 65:489-497.
- Wilkinson, G. S. 1992. Information transfer at evening bat colonies. *Animal Behavior* 44:501-518.

Figure 2.1. Locations of the Joseph W. Jones Ecological Research Center (natural site) and the Aultman Tract (managed site) study areas in southwestern Georgia used in an investigation of evening bat roost site selection in 2002 – 2003.

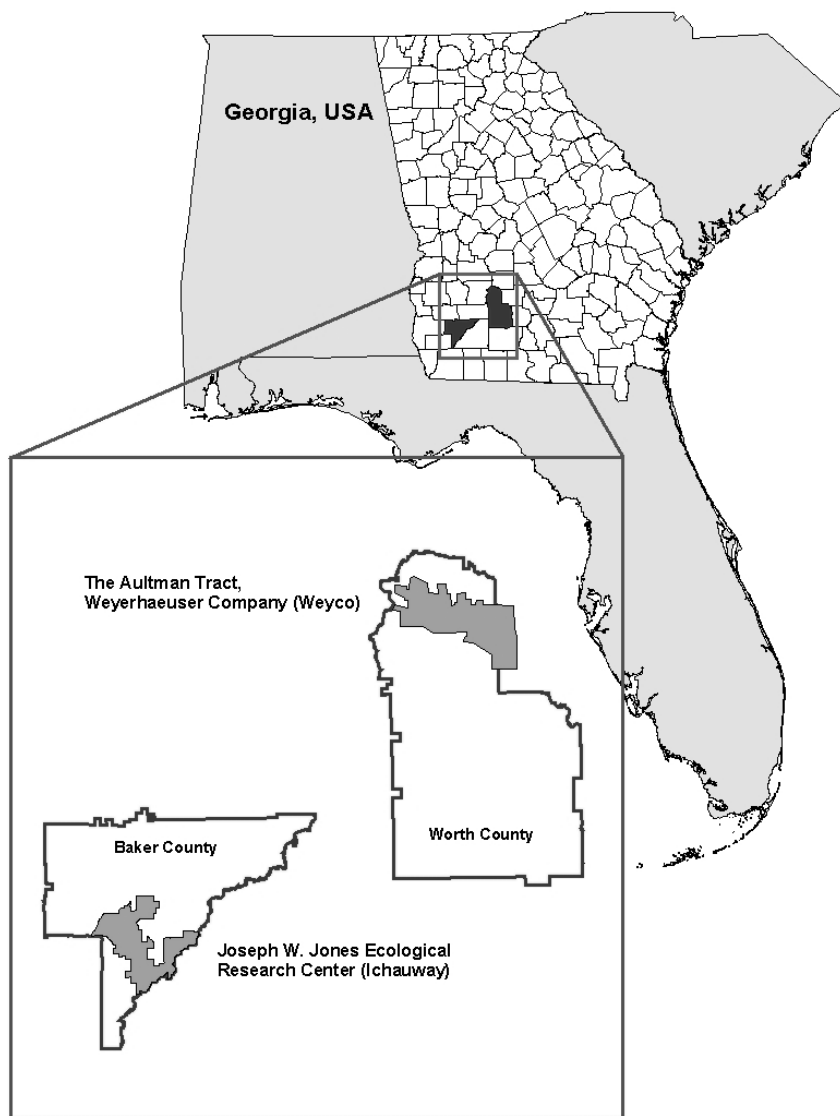
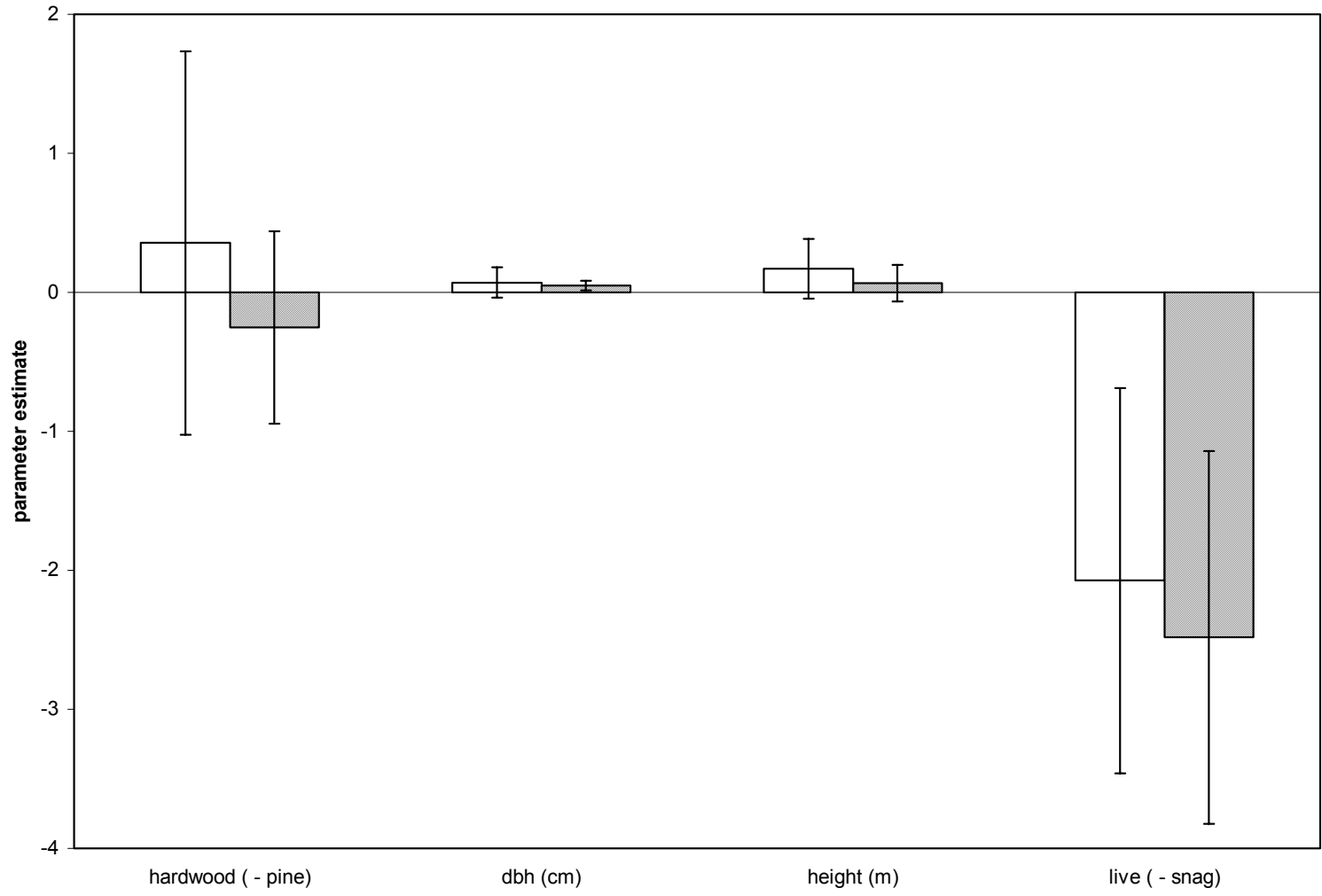
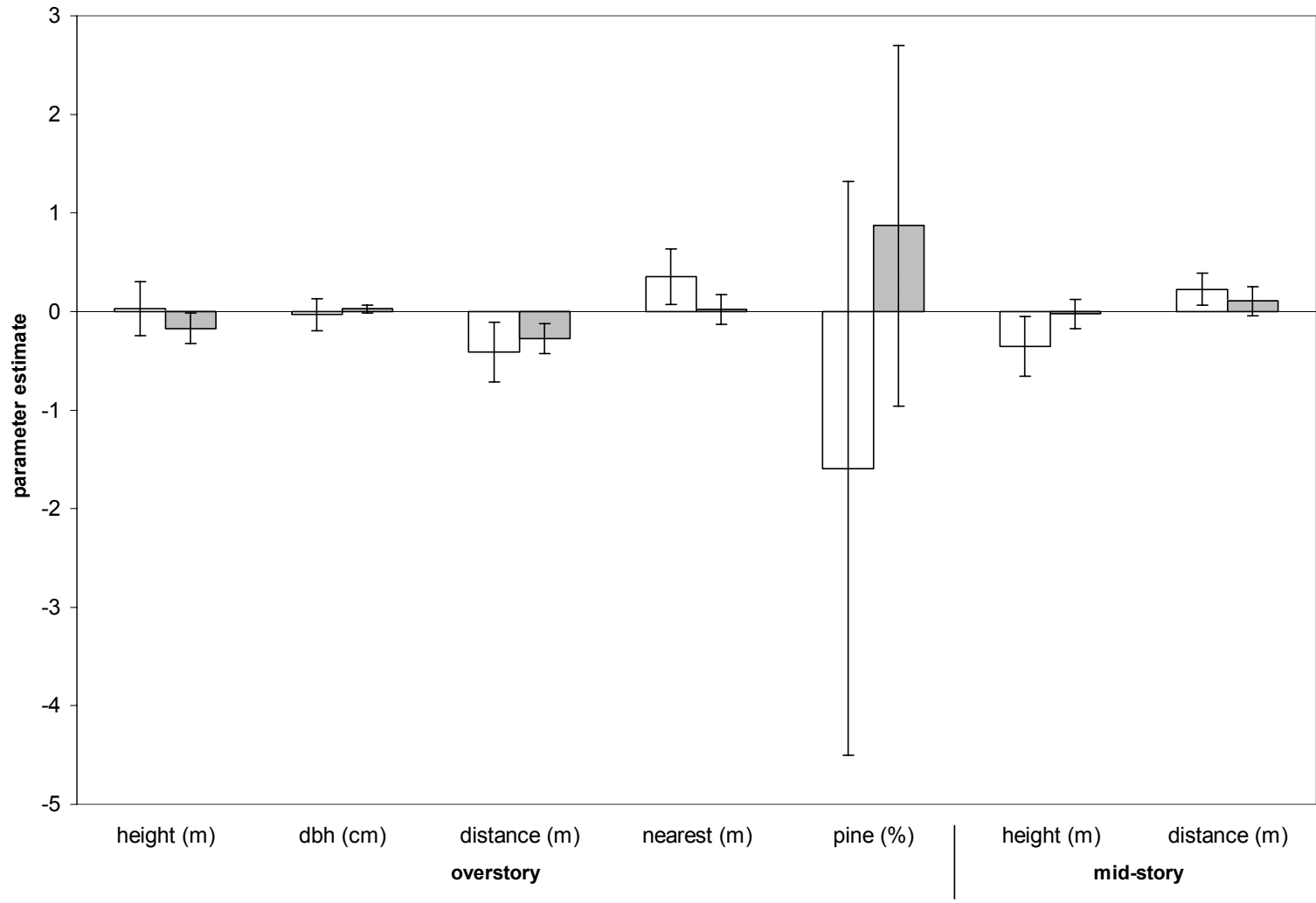


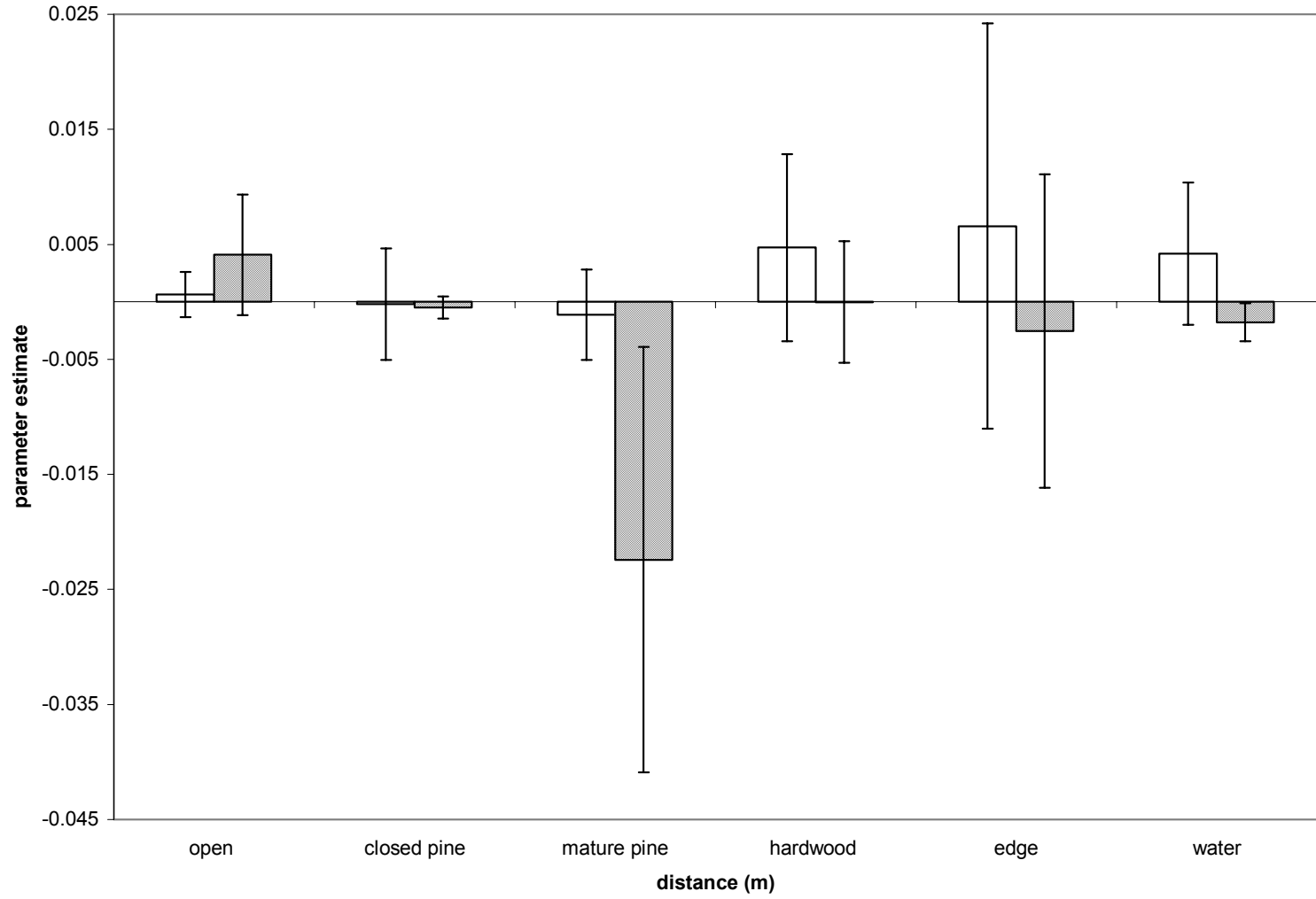
Figure 2.2. Model averaged parameter estimates and 95% CI (error bars) for variables describing the tree (a), plot (b), stand (c), and buffer (d) from multivariate logistic regression models for the managed (white) and natural (shaded) sites. Only variables describing the tree and plot were important on managed, but estimates were provided for stand and buffer variables for comparison.



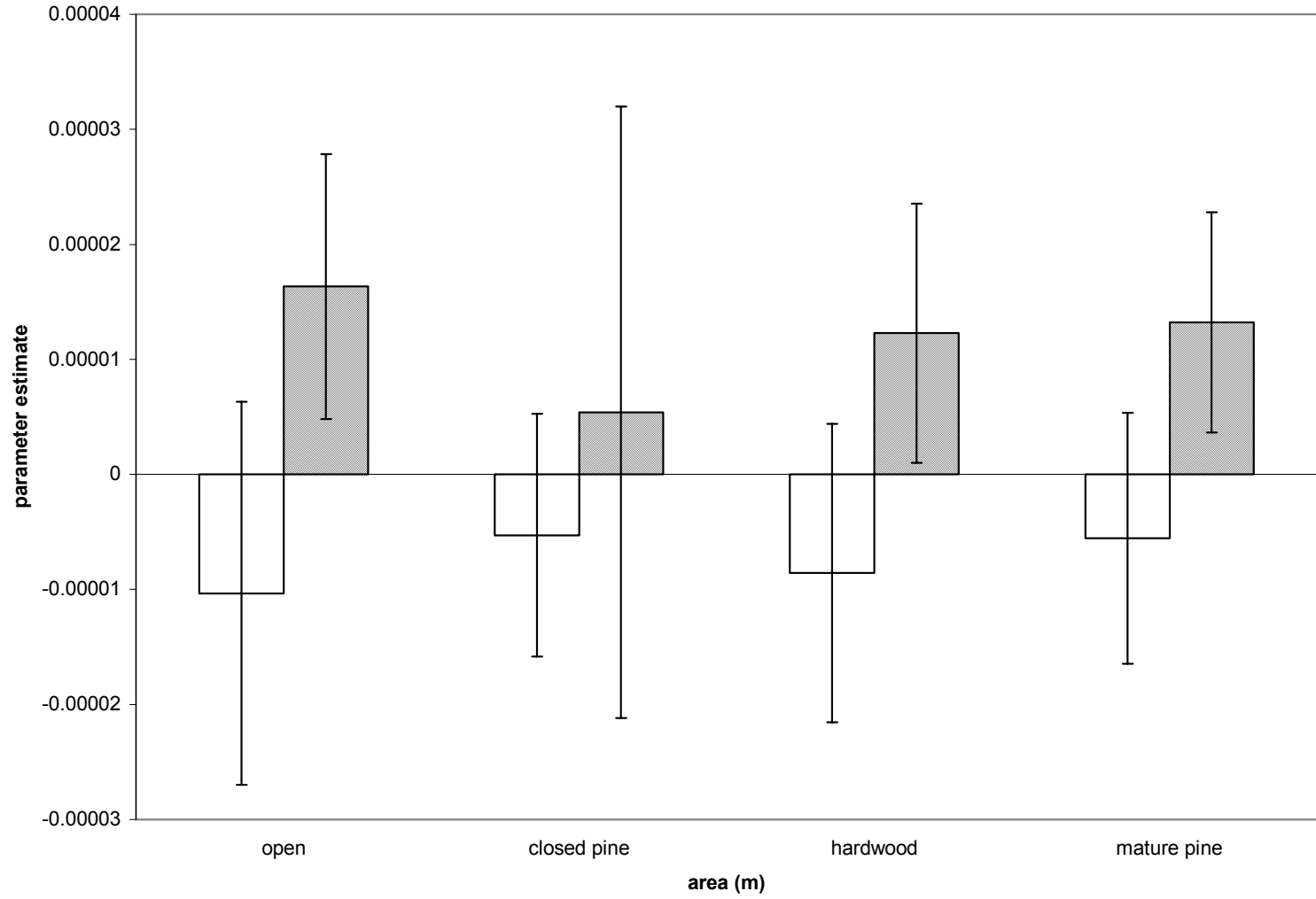
a.



b.



c.



d.

Table 2.1. Variable levels and definitions for variables measured at evening bat roost sites and random sites in southwestern Georgia, 2002-2003.

Level	Variable	Definition
TREE	hardwood (- pine)	Roost tree hardwood or pine
	dbh	Dbh (cm) of the roost tree
	height	Height (m) of the roost tree
	live (- snag)	Roost tree live or snag
PLOT	ov_height	Mean height (m) of overstory trees
	ov_dbh	Mean dbh (cm) of overstory trees
	ov_distance	Mean distance (m) to overstory trees
	ov_nearest	Distance (m) to nearest overstory tree
	ov_pine	Percent pine (%) of overstory trees
	mid_height	Mean height (m) of midstory trees
	mid_distance	Mean distance (m) to midstory trees
STAND	open	Distance (m) to open (or clear-cut) stand
	closed pine	Distance (m) to closed pine stand
	mature pine	Distance (m) to mature pine stand
	hardwood	Distance (m) to hardwood stand
	edge	Distance (m) to nearest edge or road
	water	Distance (m) to nearest water (pond or stream)
	stand size	Area (m ²) of stand
BUFF430	open	Area (m ²) of open within 430 m of tree
	closed pine	Area (m ²) of closed pine within 430 m of tree
	hardwood	Area (m ²) of hardwood within 430 m of tree
	mature pine	Area (m ²) of mature pine within 430 m of tree

Table 2.2. Means and standard errors (SE) for variables measured at evening bat roost sites on natural and managed landscapes in southwestern Georgia, 2002-2003.

Variable	Natural (<i>n</i> = 108)		Managed (<i>n</i> = 51)	
	mean	SE	mean	SE
TREE				
dbh (cm)	50.0	1.8	26.3	1.3
height (m)	22.2	0.5	15.4	0.9
PLOT				
ov_height (m)	19.7	0.4	15.4	0.7
ov_dbh (cm)	37.4	1.1	23.6	1.1
ov_distance (m)	9.8	0.4	5.1	0.6
ov_nearest (m)	5.2	0.3	3.0	0.6
ov_pine (%)	70.0	0.0	40.0	10.0
mid_height (m)	3.0	0.3	4.1	0.4
mid_distance (m)	13.0	0.3	8.2	0.7
STAND				
open (m)	100.0	9.4	392.9	40.7
closed pine (m)	659.3	39.7	176.3	17.9
mature pine (m)	7.8	2.6	98.8	19.1
hardwood (m)	91.0	8.8	60.2	13.8
edge (m)	28.0	2.8	60.3	8.3
water (m)	333.3	23.4	163.5	18.4
stand size (m ²)	180332.6	23725.3	298458.6	33160.1
BUFF430				
open (m ²)	108053.7	6972.8	19636.4	5228.4
closed pine (m ²)	7495.8	1801.2	109484.7	15426.5
hardwood (m ²)	103395.4	6637.2	177691.9	20257.8
mature pine (m ²)	334674.8	9972.9	212267.2	17984.4

Table 2.3. The best approximating logistic regression models (lowest AIC_c) out of 16 considered on the natural site ($n = 218$). Models used to predict the probability of a site being used by evening bats as a roost tree in southwestern Georgia, 2002-2003.

Model	K^a	-2 log l	AIC_c	Δ_i^b	w_i^c
TREE PLOT BUFF430	16	187.1310	221.8374	0.00	0.4017
TREE PLOT STAND BUFF430	23	170.3384	222.0291	0.19	0.3650
TREE PLOT STAND	19	181.3045	223.1428	1.31	0.2091
TREE PLOT	12	201.9699	227.4919	5.65	0.0238
TREE STAND BUFF430	16	201.8168	236.5232	14.69	0.0003
TREE STAND	12	212.7339	238.2559	16.42	0.0001
TREE BUFF430	9	220.0809	238.9463	17.11	0.0001
TREE	5	236.8582	247.1412	25.30	0.0000
NULL MODEL	1	302.1938	304.2123	82.37	0.0000

^a Number of variables in the model.

^b Distance of the model from the best model ($\Delta_i = AIC_c - \min AIC_c$).

^c The estimated probability of being the best model (Akaike weight).

Table 2.4. The best approximating logistic regression models (lowest AIC_c) out of 16 considered on the managed site ($n = 107$). Models used to predict the probability of a site being used by evening bats as a roost tree in southwestern Georgia, 2002-2003.

Model	K^a	-2 log l	AIC_c	Δ_i^b	w_i^c
TREE PLOT	12	81.9663	109.2854	0.00	0.9589
TREE PLOT STAND	19	70.0055	116.7411	7.46	0.0231
TREE PLOT BUFF430	16	79.5833	117.6277	8.34	0.0148
TREE	5	111.2230	121.8171	12.53	0.0018
PLOT	8	105.7129	123.1823	13.90	0.0009
TREE BUFF430	9	105.7896	125.6453	16.36	0.0003
TREE PLOT STAND BUFF430	23	68.0024	127.3036	18.02	0.0001
PLOT STAND	15	93.1575	128.4323	19.15	0.0001
NULL MODEL	1	148.0998	150.1379	40.85	0.0000

^a Number of variables in the model.

^b Distance of the model from the best model ($\Delta_i = AIC_c - \min AIC_c$).

^c The estimated probability of being the best model (Akaike weight).

CHAPTER 3

BAT COMMUNITY STRUCTURE AND ACTIVITY IN LONGLEAF AND LOBLOLLY
PINE FORESTS OF SOUTHWEST GEORGIA ²

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ABSTRACT

We used mist nets to investigate bat community structure and Anabat II detectors to investigate bat activity on mature longleaf pine and intensively managed loblolly pine landscapes in southwestern Georgia. Mist nets were set over ponds, small streams, and roadside ditches surrounded by a variety of habitat types. Detectors were placed in replicates of 4 habitat types (open, closed pine, hardwood, mature pine) on each study site. We captured 649 bats of six species during 83 nights (8514 net hours) of trapping at both sites. The Seminole bat (*Lasiurus seminolus*), red bat (*L. borealis*), and evening bat (*Nycticeius humeralis*) were the three most common species captured. Approximately 30% of captures on each study site were juveniles, and >97% of adult females captured showed signs of reproduction indicating that both sites provided sufficient quality habitat to allow for reproduction. Evening bats were more commonly captured on the longleaf site, while *Lasiurus* spp. were more commonly captured on the intensively managed site. Bat activity was greater in mature pine than other habitats on the longleaf site. Activity was lowest in the hardwood habitat type on the managed site, but other habitats did not differ. The continual harvest and regeneration of intensive forest management creates diverse and abundant open and edge habitat that likely provided foraging habitat for lasiurine bats on the managed site. These same processes likely reduced available roosting habitat for evening bats as reflected in lower capture rates than on the longleaf site. Management activities that reduce clutter (such as burning or thinning) in hardwood and mature pine habitat types may benefit common species on intensively managed landscapes.

INTRODUCTION

The longleaf pine forest ecosystem once covered over 37 million hectares in the southeastern United States, but currently has been reduced to less than 1.2 million hectares

(Landers et al. 1995). Conversely, to meet demands for forest products, the area covered by managed pine plantations in the South is expected to increase 67% from 12 million hectares in 1999 to 20 million hectares by 2040 (Wear and Greis 2002). The intensive management of these forests result in short rotations, loss of late successional forests, and may result in declines in species diversity of vegetation communities (Allen et al. 1996).

Nine of the 18 species of southeastern bats may be directly affected by forest management practices because they rely on forests for their primary roosting and foraging sites (Brown 1997, Carter 1998). Bat species differ in their ability to adapt to changes in forest structure because of differing degrees of morphological and behavioral specialization. Management practices that limit available roosting structures may result in changes in species composition or elimination of species with specific roosting requirements (Humphrey 1975). Alterations to foraging habitat may be detrimental because selection of foraging habitat often is based on morphological and echolocation characteristics of species (Findley 1976, Sherwin et al. 2000, Patriquin and Barclay 2003). Over large spatial scales, the landscape scale changes in forest structure associated with the shift from historic longleaf conditions to intensively managed landscapes could result in changes of bat communities in the region. However, few studies have attempted to document bat community structure and foraging habitat associations in longleaf or intensively-managed pine landscapes in the Southeast.

Mist net surveys are commonly employed to examine bat community structure throughout North America (Murray et al. 1999, O'Farrell and Gannon 1999). The direct capture of individuals allows positive species identification, reproductive assessment, and estimation of sex and age ratios (Murray et al. 1999, Miller 2003). Previous surveys in the Southeast suggest that the bat community is dominated by a few common species (Seminole, red, and evening bats)

(Humphrey 1975, Carter 1998, Miller 2003). Capture records also have been reported in different forest types including hardwood dominated (Owen 2000), mature longleaf pine (Carter 1998), and intensively managed (Miller 2003) landscapes throughout the region.

Bat detectors have been used to examine relative activity of foraging bats in relation to different forest management practices (Furlonger et al. 1987, Grindal and Brigham 1999, Owen 2000, Menzel et al. 2002). Studies have demonstrated the importance of old growth or mature forests (Crampton and Barclay 1998, Humes et al. 1999), edge (Menzel et al. 2002) and open (Menzel et al. 2002, Erickson and West 2003) habitats to bats. Habitat associations have been linked to foraging strategies and morphological characteristics of bat species or guilds (Patriquin and Barclay 2003). Acoustic detections of aerial foraging (aerial hawking) species are greater in open and edge habitats where quick flight can be used to capture prey (Patriquin and Barclay 2003). Habitat types with clutter are avoided by aerial hawking species, but are regularly used by species which forage insects off of vegetation (gleaners, Patriquin and Barclay 2003)

To provide information on bat community structure and foraging habitat use in pine forests of the Southeast, our objectives were to: (1) describe bat community structure, and (2) compare the relative activity of foraging bats among habitat types within intensively managed loblolly and mature longleaf pine landscapes.

STUDY AREA

We conducted the study in the Upper Coastal Plain physiographic region of southwestern Georgia, between 31°50' and 31°4' N latitude and 84°40' and 83°39' W longitude. This region is characterized by hot, humid summers with average daily temperatures of 27° C. Afternoon thunderstorms occurred frequently in summer and average annual precipitation was 132 cm/year.

We selected two sites for study, one that represented the historic longleaf condition and one that represented an intensively managed pine landscape (Figure 2.1). The Joseph W. Jones Ecological Research Center at Ichauway (natural site), in Baker County, Georgia was a 12,000-ha research site managed with biennial prescribed fire to simulate natural disturbance patterns and promote a landscape similar to the historic longleaf pine ecosystem. Longleaf forests were between 70 to 90 years old, with individual trees >300 years old scattered throughout the site. Southern red oak (*Quercus falcata*), sweetgum (*Liquidambar styraciflua*), and other hardwoods commonly occurred individually within mature pine forests. Snags (especially pine, to a lesser extent hardwoods) were also common in forested areas. Riparian hardwood forests, mixed pine/hardwood forests, and wildlife openings were scattered throughout the site.

The Aultman Tract (managed site), in Worth County, Georgia, approximately 70 km to the northwest of Ichauway, was a 14,000-ha area consisting primarily of loblolly pine plantations managed by Weyerhaeuser Company for sawtimber on a 30-year rotation. Typical management for pine stands included site preparation and planting, vegetation management, commercial thinning, pruning, and fertilization. This management resulted in even-aged stands of different successional stages distributed in a mosaic throughout the landscape. A dense hardwood midstory of sweetgum, persimmon (*Diospyros virginiana*), and oaks often were present in stands between 20 to 30 years old. Interspersed throughout the site were non-plantation habitats >50 years old including streamside management zones, mature pine-hardwood and hardwood forests.

METHODS

We captured bats from May to early-September 2002 and 2003 with 6 m to 18 m x 2.4 m mist nets set over ponds, small streams, and roadside ditches surrounded by a variety of habitats throughout each study site. Captured bats were identified to species, and mass (g), forearm

length (mm), sex, age (Anthony 1988), and reproductive condition (Racey 1988) were recorded. We compared bats/trap-hour between sites using a *t*-test with each sample night as the experimental unit. We defined trap hours as the time mist nets were opened at a capture site. We used Simpson's diversity index (1-D, probability that two bats drawn at random will be the same species) and sex ratios to describe bat community structure on each study site (Miller 2003).

We used a geographic information system (GIS, ArcInfo, Environmental Systems Research Institute, Redlands, California, USA) to divide each study area into four habitat types (mature pine, closed pine, open, hardwood). Habitat definitions were simplified for consistency between sites. Mature pine included upland stands where pine dominated the canopy on the natural site and thinned pine stands (approx 13 to 30 years old) on the managed site. Closed pine stands were young, dense stands with almost complete canopy closure. Open habitat on the natural site included fields and wildlife food plots, and primarily clear cuts and regeneration stands <8 years old on the managed site. Hardwood included upland hardwood and mixed pine hardwood (hardwood dominated) stands, riparian areas, and cypress/forested wetlands on each site. Most hardwood areas on the managed site were designated as reserve areas and received limited management.

We recorded bat activity in habitat designations using Anabat II bat detector systems (Titley Electronics, Ballina, New South Wales, Australia) placed at 1.5 m on a tripod angled at 30 degrees (Weller and Zabel 2002). An Anabat II detector system included an Anabat II detector and a CF-Storage ZCAIM (Titley Electronics) placed in a waterproof plastic box. Prior to sampling, we calibrated bat detectors relative to one another using SONIN 60 PRO electronic distance-measuring tool (SONIN, Scarsdale, New York, USA)(Larson and Hayes 2000, Weller

and Zabel 2002). On each night sampled, detectors were placed in all four habitat types on one study area and set to automatically record simultaneously from dusk till dawn. We moved detectors to a new set of replicate habitat types each night. Detector locations were determined by selecting an opening near a random point generated in the GIS. We placed detectors in openings to minimize the effect of clutter on the area sampled in different habitat types (Hayes 2000, Weller and Zabel 2002).

Files from the CF-Storage ZCAIM were downloaded to a computer for analysis. We separated files containing bat calls from those containing insect and extraneous noise using a custom filter in Analook software (Version 4.8, Titley Electronics)(Britzke and Murray 2000). Files were then manually checked for accuracy. Bat activity was defined as bat passes per hour. We defined a bat pass as a file which contained >2 clearly defined echolocation pulses. We compared bat activity among habitat types on each study area using a one-way ANOVA on ranked data, and used Tukey's multiple mean comparison to distinguish which means differed (SAS Institute, Cary, N.C.).

RESULTS

We captured 649 bats of six species during 83 nights (8514 net hours) of trapping at both study sites (Table 3.1). We captured 286 bats of six species in 110 hours on 18 sites in the natural landscape and 315 bats of five species in 129 hours on 31 sites in the managed landscape. Trap effort was not equal between study sites because our main objective was to capture and attach radio transmitters to evening bats for a separate study. The southeastern myotis (*Myotis austroriparius*) was only captured on the natural site ($n = 6$). The Seminole bat (47%, $n = 306$) was the most common species captured on each site followed by the red bat (26%, $n = 169$), and evening bat (22%, $n = 144$). Simpson's diversity index (1-D) was 0.636 on the natural site and

0.617 on the managed site. We captured 1.2 ± 0.18 (mean \pm se) evening bats per hour on the natural site and 0.71 ± 0.15 on the managed site (t -test, $t_{44} = 2.23$, $P = 0.03$). However, foliage roosting bats (*Lasiurus* spp.) were more commonly captured on the managed site (2.2 ± 0.31 per hour) than the natural site (1.4 ± 0.27 per hour, t -test, $t_{80} = 2.09$, $P = 0.04$).

Sex ratios were skewed toward females for adult Seminole (natural = 4.3F:M, managed = 7.5F:M) and red bats (natural = 6.3F:M, managed = 37F:M). Evening bat sex ratios were female dominated on the natural (2.2F:M) site and close to even on the managed (1.3F:M) site. Ninety seven percent ($n = 313$) of adult females on both study sites showed active signs of reproduction (pregnant, lactating, or post-lactating). Juvenile bats represented 33% ($n = 87$) of captures on the natural site and 30% ($n = 95$) of captures on the managed site.

We recorded 3420 bat passes on 18 nights in the natural site and 2367 bat passes on 16 nights in the managed site. Detectors operated 7 ± 0.79 (range 2.5 – 10.6) hours per night on the natural site and 8 ± 0.92 (range 2.1 – 10.6) hours per night on the managed site. We recorded 6.5 ± 1.1 bat passes per hour on the natural site and 4.3 ± 0.76 passes per hour on the managed site. On the natural site, mature pine had between 1 and 18 passes per hour more than other habitat types ($F_{3,68} = 8.05$, $P = 0.0001$, Figure 3.2). On the managed site, mature pine (6.8 ± 2.2 passes per hour), open (4.9 ± 0.9), and closed canopy pine (3.9 ± 1.6) had greater activity than hardwood (1.5 ± 0.5) forest ($F_{3,60} = 5.08$, $P = 0.0034$, Figure 3.2).

DISCUSSION

Bat community structure was similar between the natural and managed landscapes. Our bat captures were dominated by three common species (Seminole bat, red bat, and evening bat). The Seminole bat, red bat, and evening bat were also the most commonly captured species in other studies in the southeastern United States (Lance and Garrett 1997, Menzel et al. 1999,

Miller 2003). Although we had no data on recruitment, virtually all of the adult females captured showed signs of reproduction, and we frequently captured juvenile bats, suggesting both study sites provided sufficient quality habitat to allow for reproduction (Miller 2003).

Despite a similar community structure, capture rates of the common species differed between the study sites. We captured more evening bats per hour on the natural site, and more *Lasiurus* spp. per hour on the managed site. We assumed that species capture probabilities were equal between the study sites, but could not formally test this assumption. Though there are many potential explanations for the difference in capture rates of common species between the study sites, differences could be related to roosting and foraging habitat preferences. The availability of suitable roosting structures may be a limiting factor for species with specific roosting requirements (Humphrey 1975). Evening bats roost under exfoliating bark or in cavities of living or dead trees (Menzel et al. 2000, 2001). Due to the short rotation of pine stands on the managed site, availability of suitable roosting structures likely was more limited whereas large trees and snags were common across the landscape on the natural site. In contrast, lasiurine bats roost in the foliage of hardwood and pine trees (Menzel et al. 2000). Both study sites likely provide adequate roosting habitat for foliage roosting species. Differences in foraging habitat may be contributing to the difference in lasiurine capture rates between the study sites. *Lasiurus* spp. typically forage over open and edge habitats (Menzel et al. 2002). The continual harvest and regeneration of intensive forest management creates diverse and abundant open and edge habitats that likely provides foraging habitat for lasiurine bats.

The mature pine habitat type had the greatest bat activity on the natural site. The mature longleaf pine stands were burned on a 2-year fire rotation, resulting in open, park like stands with little midstory. The importance of non-cluttered habitats to many bat species, especially aerial

hawkers, has been noted by other researchers (Brigham and Fenton 1986, Grindal and Brigham 1999, Kalcounis et al. 1999). The mature pine stands on the managed site often had a dense hardwood midstory. The dense midstory may have decreased bat activity in these stands (relative to other habitat types) because of increased clutter. Hardwood habitats had the least activity on the managed site. High amounts of clutter associated with this habitat type likely reduced its value as foraging habitat. However, two of the common species (red bat and evening bat) frequently roost in hardwood habitat types (Menzel et al. 2000). Thus these areas may be important roosting areas for bats despite the limited foraging activity observed

Bat activity measured with bat detectors is highly variable both spatially and temporally (Hayes 1997, Sherwin et al. 2000, Weller and Zabel 2002). We controlled for spatial and temporal variability by simultaneously sampling habitat types of interest within a study area and sampling multiple replicates of each habitat type throughout the summer. We did not simultaneously sample the two study sites, therefore we did not make direct comparisons of habitat associated bat activity between the study sites.

We assumed equal detection probabilities between habitat types during each sampling period (Sherwin et al. 2000), although we had no formal method of testing this assumption. Britzke (2003) noted that detection probabilities between open and cluttered habitat types were not equal, and Weller and Zabel (2002) noted large variations in activity at a single location within a forest depending on orientation of bat detectors. We attempted to reduce potential bias by orientating all detectors toward openings within each habitat type. Cluttered habitats (forested stands) received the highest activity on both study sites, indicating that if the assumption of equal detection probability between habitats was violated, the effect was not strong enough to affect results.

We did not attempt to identify bat passes to species because we were unable to create a large enough library of reference calls specific to the habitat types in our study area. In a comparison of mist net and bat detector species assemblages, Murray et al. (1999) found that more species were detected acoustically than with mist nets. Therefore, it is possible that species that were rarely or not captured in mist nets may have been detected in the study sites acoustically, but were not identified. However, Owen (2000) found that the most common species captured in mist nets were also the most commonly detected species in his study areas. Given the simple bat community present on the study area, we assume that the majority of calls recorded were from the three most common species (Seminoe bat, red bat, and evening bat).

The natural and managed study sites had similar bat communities and provided habitat of sufficient quality to allow for reproduction. We suggest that differences in capture rates of common species are related to habitat conditions of the sites. Because we only conducted the study on two study sites, our inferential space is limited to the landscapes in which we conducted the study. The results of this study should be used in conjunction with previous and future research in the region to create management recommendations. Management activities that reduce clutter (such as burning or thinning) may benefit the common bat species on intensively managed landscapes.

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LITERATURE CITED

- Allen, A. W., Y. K. Bernal, and R. J. Moulton. 1996. Pine plantations and wildlife in the Southeastern United States: an assessment of impacts and opportunities. U.S. Department of the Interior, Information and Technology Report. National Biological Service, Washington, D.C., USA.
- Anthony, E. L. P. 1988. Age determination in bats. Pages 47-55 *in* T. H. Kunz, editor. Ecology and behavioral methods for the study of bats. Smithsonian Institution Press, Washington, D.C., USA.
- Brigham, R. M., and M. B. Fenton. 1986. The influence of roost closure on the roosting and foraging behavior of *Eptesicus fuscus* (Chiroptera: Vespertilionidae). Canadian Journal of Zoology 64:1128-1133.
- Britzke, E. R. 2003. Use of ultrasonic detectors for acoustic identification and study of bat ecology in the eastern United States. Dissertation, Tennessee Technological University, Cookeville, USA.
- Britzke, E. R., and K. L. Murray. 2000. A quantitative method for selection of identifiable search-phase calls using the Anabat system. Bat Research News 41:33-36.
- Brown, L. N. 1997. A guide to the mammals of the southeastern United States. University of Tennessee Press, Knoxville, USA.
- Carter, T. C. 1998. The foraging ecology of three species of bats at the Savannah River Site, South Carolina. Thesis, University of Georgia, Athens, USA.

- Crampton, L. H., and R. M. R. Barclay. 1998. Selection of roosting and foraging habitat by bats in different-aged aspen mixedwood stands. *Conservation Biology* 12:1347-1358.
- Erickson, J. L., and S. D. West. 2003. Associations of bats with local structure and landscape features of forested stands in western Oregon and Washington. *Biological Conservation* 109:95-102.
- Findley, J. S. 1976. The structure of bat communities. *The American Naturalist* 110:129-139.
- Furlonger, C. L., H. J. Dewar, and M. B. Fenton. 1987. Habitat use by foraging insectivorous bats. *Canadian Journal of Zoology* 65:284-288.
- Grindal, S. D., and R. M. Brigham. 1999. Impacts of forest harvesting on habitat use by foraging insectivorous bats at different spatial scales. *Ecoscience* 6:25-34.
- Hayes, J. P. 1997. Temporal variation in activity of bats and the design of echolocation-monitoring studies. *Journal of Mammalogy* 78:514-524.
- Hayes, J. P. 2000. Assumptions and practical considerations in the design and interpretation of echolocation-monitoring studies. *Acta Chiropterologica* 2:225-236.
- Humes, M. L., and J. P. Hayes, and M. W. Collopy. 1999. Bat activity in thinned, unthinned, and old-growth forests in western Oregon. *Journal of Wildlife Management* 63:1999.
- Humphrey, S. R. 1975. Nursery roosts and community diversity of nearctic bats. *Journal of Mammalogy* 56:321-346.
- Kalcounis, M. C., K. A. Hobson, R. M. Brigham, and K. R. Hecker. 1999. Bat activity in the boreal forest: importance of stand type and vertical strata. *Journal of Mammalogy* 80:673-682.
- Lance, R. F., and R. W. Garret. 1997. Bat fauna of central Louisiana forests. *Texas Journal of Science* 49:181-189.

- Landers, J. L., D. H. Van Lear, and W. D. Boyer. 1995. The longleaf pine forests of the Southeast: requiem or renaissance. *Journal of Forestry* 93:39-44.
- Larson, D. J., and J. P. Hayes. 2000. Variability in sensitivity of Anabat II bat detectors and a method of calibration. *Acta Chiropterologica* 2:208-213.
- Menzel, M. A., D. M. Krishon, T. C. Carter, and J. Laerm. 1999. Notes on tree roost characteristics of the northern yellow bat (*Lasiurus intermedius*), the Seminole bat (*L. seminolus*), the evening bat (*Nycticeius humeralis*), and the eastern pipistrelle (*Pipistrellus subflavus*). *Florida Scientist* 62:185-193.
- Menzel, M. A., T. C. Carter, W. M. Ford, and B. R. Chapman, and J. Ozier. 2000. Summer roost tree selection by eastern red, Seminole, and evening bats in the upper Coastal Plain of South Carolina. *Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies* 54:304-313.
- Menzel, M. A., T. C. Carter, W. M. Ford, and B. R. Chapman. 2001. Tree roost characteristics of subadult and female adult evening bats (*Nycticeius humeralis*) in the upper coastal plain of South Carolina. *American Midland Naturalist* 145:112-119.
- Menzel, M. A., T. C. Carter, J.M. Menzel, W. M. Ford, and B. R. Chapman. 2002. Effects of group selection silviculture in bottomland hardwoods on the spatial activity patterns of bats. *Forest Ecology and Management* 162:209-218.
- Miller, D.A. 2003. Species diversity, reproduction, and sex ratios of bats in managed pine forest landscapes of Mississippi. *Southeastern Naturalist* 2:59-72.
- Murray, K. L., E. R. Britzke, B. M. Hadley, and L. W. Robbins. 1999. Surveying bat communities: a comparison between mist nets and the Anabat II bat detector system. *Acta Chiropterologica* 1:105-112.

- O'Farrell, M. J., and W. L. Gannon. 1999. A comparison of acoustic versus capture techniques for the inventory of bats. *Journal of Mammalogy* 80:24-30.
- Owen, S. F. 2000. Impacts of timber harvest in the central Appalachians hardwood region on bat foraging and roosting behavior. Thesis, University of Georgia, Athens, USA.
- Patriquin, K. J., and R. M. R. Barclay. 2003. Foraging by bats in cleared, thinned, and unharvested boreal forest. *Journal of Applied Ecology* 40:646-657.
- Racey, P. A. 1988. Reproductive assessment in bats. Pages 31-43 *in* T. H. Kunz, editor. *Ecology and behavioral methods for the study of bats*. Smithsonian Institution Press, Washington, D.C., USA.
- Sherwin, R. E., W. L. Gannon, and S. Haymond. 2000. The efficacy of acoustic techniques to infer differential use of habitat by bats. *Acta Chiropterologica* 2:145-153.
- Wear, D. N., and J. G. Greis. 2002. The southern forest resource assessment: Summer, Report. U. S. Department of Agriculture, Forest Service, General Technical Report SRS-54.
- Weller, T. J., and C. J. Zabel. 2002. Variation in bat detections due to detector orientation in a forest. *Wildlife Society Bulletin* 30:922-930.

Figure 3.1. Locations of the Joseph W. Jones Ecological Research Center (natural site) and the Aultman Tract (managed site) study areas in southwestern Georgia used to investigate bat community structure and bat activity from May to September 2002-2003.

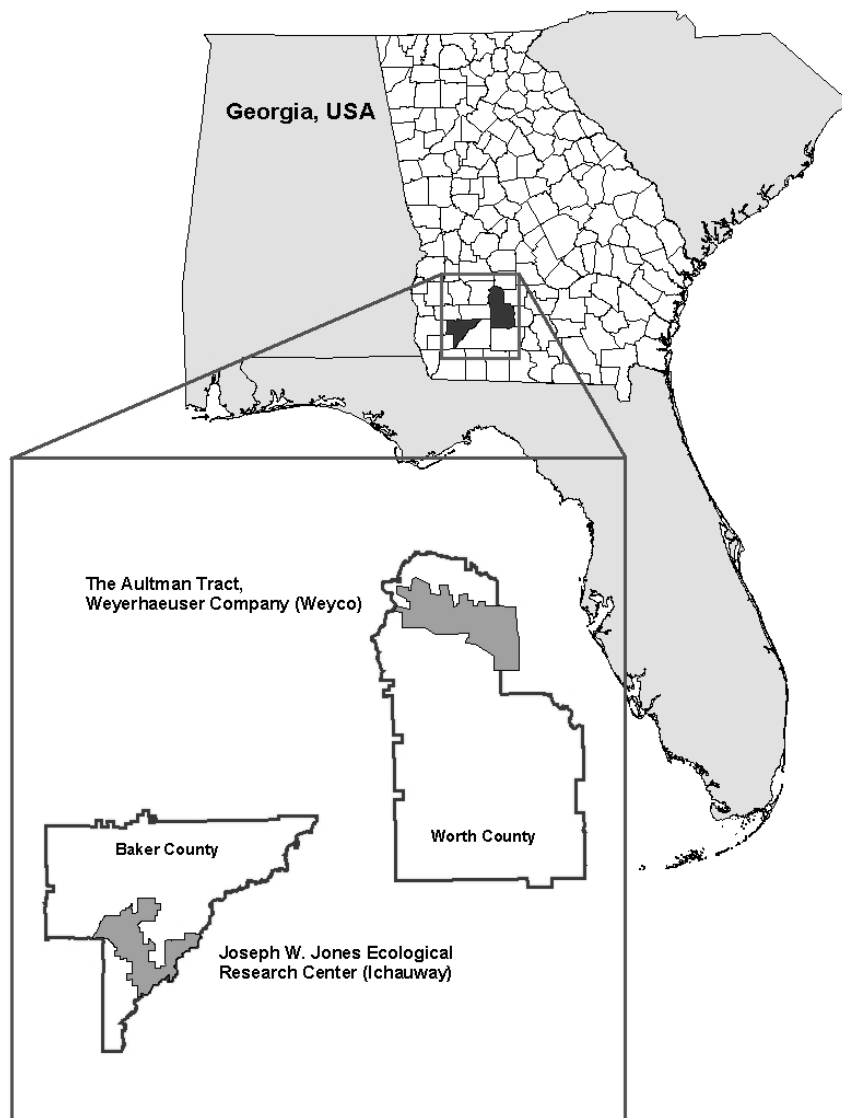


Figure 3.2. Bat activity (passes/hour) recorded with bat detectors in replicates of four habitat types on natural (n=18) and managed (n=16) sites in southwestern Georgia during summer 2003.

Error bars indicate 95% confidence intervals.

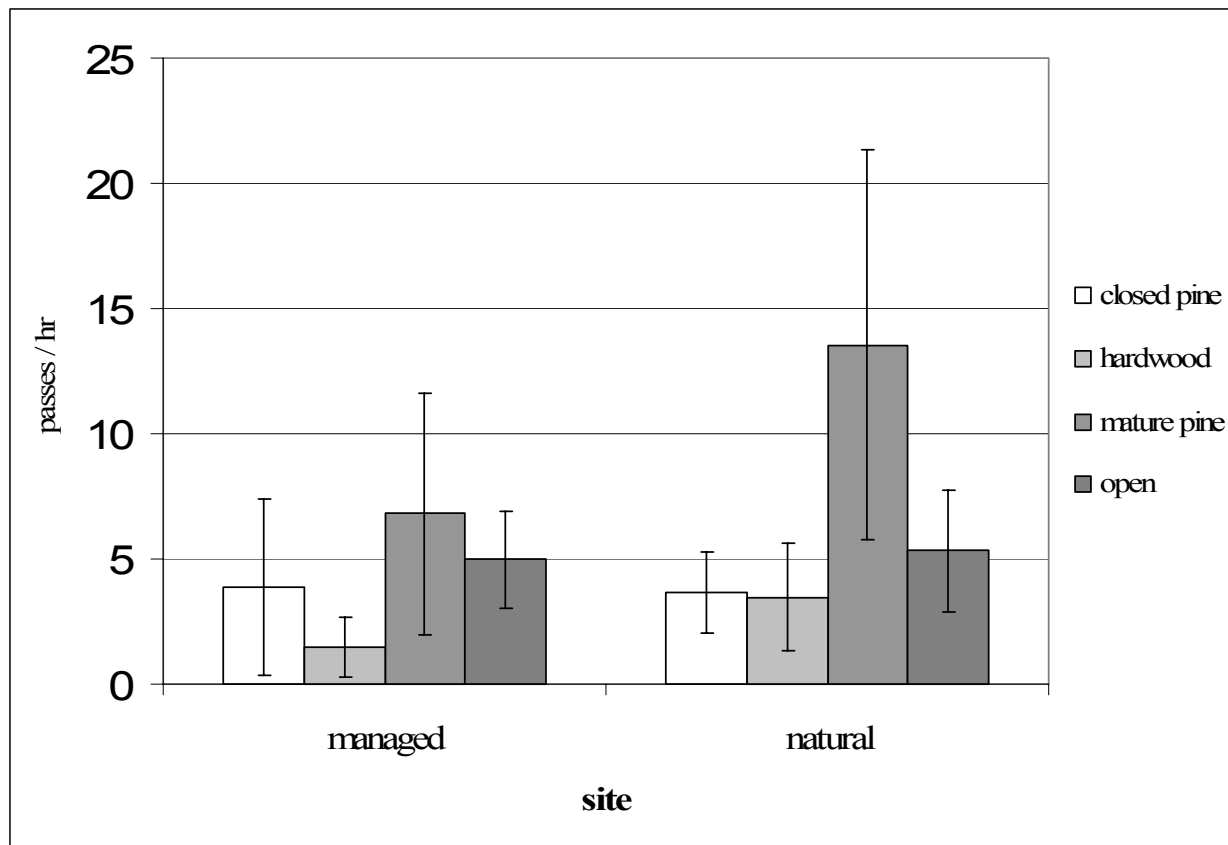


Table 3.1. Sex and age of bats captured during 110 trap hours on natural (3826 net hours) and 129 trap hours on managed (4689 net hours) pine forest landscapes in southwestern Georgia, 2002-2003.

	Natural				Managed			
	male	female	juvenile	total ^a	male	female	juvenile	total ^a
Evening bat (<i>Nycticeius humeralis</i>)	26	56	15	98	16	21	9	46
Eastern red bat (<i>Lasiurus borealis</i>)	3	19	14	37	2	74	39	132
Seminole bat (<i>Lasiurus seminolus</i>)	13	56	51	136	12	90	45	170
<i>Lasiurus</i> sp. ^b	0	0	0	2	0	0	0	8
Southeastern myotis (<i>Myotis austroriparius</i>)	1	1	4	6	0	0	0	0
Eastern pipistrelle (<i>Pipistrellus subflavus</i>)	1	2	1	4	1	3	1	5
Brazilian free-tailed bat (<i>Tadarida brasiliensis</i>)	1	0	2	3	0	1	1	2
Total	45	134	87	286	31	189	95	363

^a Includes bats that escaped before sex and age could be determined.

^b Seminole or red bats that escaped before positive identification to species.

CHAPTER 4

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

The longleaf pine (*Pinus palustris*) ecosystem historically dominated the Coastal Plain of the southeastern United States (Landers et al. 1995). Longleaf forests likely provided abundant habitat for a variety of bat species because large trees and snags were abundant throughout the landscape for roosting, and forests had open canopy structure for foraging. Natural longleaf pine forests have been drastically reduced while intensively managed loblolly pine (*P. taeda*) plantations have increased in the Southeast (Wear and Greis 2002). Intensively managed pine plantations have short rotation times (<30 years) which results in loss of late successional forests characteristics and declines in species diversity of vegetation communities (Allen et al. 1996). Conservation of biodiversity in both the remaining longleaf pine forests and intensively managed pine forests in the Southeast is critical, yet information on bats in these landscapes is limited. The objectives of this research were to: (1) examine the roost site selection of evening bats in relation to forest management, and (2) describe bat community structure and compare the relative activity of foraging bats among habitat types within intensively managed loblolly and mature longleaf pine landscapes.

Evening bats roosted in a variety of structures, but live conifers (*Pinus* sp. and *Taxodium distichum*) were the most common type of tree used in both mature longleaf and managed loblolly landscapes. Evening bats were more abundant, formed larger maternity colonies,

roosted closer to their capture pond, and used more roosts on the mature longleaf landscape. Multi-scale roost selection models indicated that there were differences in roost selection between the sites. Evening bats on the longleaf site selected roosts based on tree, plot, and landscape scale characteristics, while bats on the managed site selected roosts based on only the tree and plot scale. I hypothesize that greater availability of roosting structures (abundant large trees and snags) throughout the mature longleaf pine landscape allowed evening bats to select roost sites that had more favorable landscape characteristics (i.e. closer to water and foraging sites). On the managed site, favorable roosting sites were more limited, and evening bats were unable to select roosts with favorable landscape characteristics.

Though live conifers were the most frequently used roost structure, snags were selected as roost structures in greater proportion to their availability on both study sites. On the natural site, evening bats selected trees that were larger and surrounded by a shorter forest canopy than random trees. On the managed site, evening bats selected trees surrounded by an open midstory. Due to the differences in roosting ecology of evening bats between the mature longleaf and intensively managed landscapes, I recommend management actions that will increase roosting structures for evening bats on managed landscapes. The creation and preservation of streamside management zones and hardwood reserves, and leaving fork-topped loblolly pines in upland stands should improve roost availability on intensively managed forests.

The Seminole bat (*Lasiurus seminolus*), red bat (*L. borealis*), and evening bat (*Nycticeius humeralis*) were the three most commonly captured species on both study sites. High rates of reproductive females suggest that both study sites provided sufficient quality habitat to allow for reproduction. Bat activity on the longleaf site was greatest in mature pine stands, which were burned on a 2-year fire rotation and had an open, park-like structure with little midstory. Bat

activity on the managed site was lowest in the hardwood habitat type, but mature pine, closed pine, and open habitats did not differ. Differences in bat activity among habitat types on each site reflect the avoidance of heavily cluttered habitats by aerial foraging bat species.

Management activities that reduce clutter (such as burning or thinning) may benefit the common bat species on intensively managed landscapes.

Because I only investigated evening bat roosting ecology, bat community structure, and activity on one site representing each landscape type, the inferential space of the study is limited. The 2-year prescribed fire prescriptions, preservation of pine snags, and mature nature of pine stands on the longleaf site likely created ideal roosting conditions for evening bats. Although further study is warranted, we would expect to find similar results at other locations in the region with similar stand conditions. We should not expect industrial timberlands to provide the same quality or quantity of habitat for cavity roosting bats because management objectives dictate intensive management approaches that are not conducive to establishment or maintenance of snags or old trees. The similarities in community structure, greater capture rate of *Lasiurus* spp., and the identification of evening bat roosting structures suggest that intensively managed forests provide multiple bat species with foraging and roosting habitat. Additional research in other intensively managed forests should be used to corroborate these results.

This research also highlights the importance of investigating bat habitat use in landscapes with a range of forest conditions within a geographic area of interest. Had only one study site or forest condition been investigated, conclusions regarding evening bat roost selection would have been incomplete. To gain an understanding of bat roosting ecology, investigations need to be conducted throughout the range of forest conditions in which that species exist. The results of this study should be viewed in collaboration with past and future research on evening bats to gain

a fuller understanding of their roosting ecology. The landscape scale approach to investigating roost site selection introduced in this study may be valuable for examining the roosting ecology of other bat species in other regions.

LITERATURE CITED

- Allen, A. W., Y. K. Bernal, and R. J. Moulton. 1996. Pine plantations and wildlife in the Southeastern United States: an assessment of impacts and opportunities. U.S. Department of the Interior, Information and Technology Report. National Biological Service, Washington, D.C., USA.
- Landers, J. L., D. H. Van Lear, and W. D. Boyer. 1995. The longleaf pine forests of the Southeast: requiem or renaissance. *Journal of Forestry* 93:39-44.
- Wear, D.N., and J.G. Greis. 2002. The southern forest resource assessment: Summer, Report. United States Department of Agriculture, Forest Service, General Technical Report SRS-54.

APPENDIX A

MODEL AVERAGED PARAMETER ESTIMATES OF PREDICTOR VARIABLES FOUND
IN ROOST SELECTION MODELS

Appendix A.1. Model averaged parameter estimates, unconditional standard errors, odds ratios and sum of Akaike weights of predictor variables found in logistic regression models of evening bat roost site selection on the managed site.

Level	Variable	Estimate	SE	Odds ratio	Σw_i
TREE	hardwood (- pine)	0.3547	0.704	1.42573	0.9990
	dbh	0.0707	0.056	1.07326	0.9990
	height	0.1694	0.110	1.18454	0.9990
	live	-2.0735	0.707	0.12574	0.9990
PLOT	ov_height	0.0283	0.141	1.02874	0.9979
	ov_dbh	-0.0330	0.081	0.96756	0.9979
	ov_distance	-0.4125	0.155	0.66201	0.9979
	ov_pine	-1.5938	1.485	0.20315	0.9979
	mid_height	-0.3536	0.155	0.70217	0.9979
	mid_distance	0.2258	0.081	1.25338	0.9979
	ov_nearest	0.3529	0.145	1.42320	0.9979
	STAND	open	0.0006	0.001	1.00064
	closed pine	-0.0002	0.002	0.99980	0.0233
	mature pine	-0.0011	0.002	0.99889	0.0233
	hardwood	-1.20E-05	0.004	1.00473	0.0233
	edge	0.0066	0.009	1.00660	0.0233
	water	0.0042	0.003	1.00420	0.0233
	stand size	-4.84E-06	1.99E-06	1.00000	0.0233
BUFF430	open	-1.04E-05	8.50E-06	0.99999	0.0152
	closed pine	-5.29E-06	5.38E-06	0.99999	0.0152
	hardwood	-8.58E-06	6.63E-06	0.99999	0.0152
	mature pine	-5.56E-06	5.56E-06	0.99999	0.0152

Appendix A.2. Model averaged parameter estimates, unconditional standard errors, odds ratios and sum of Akaike weights of predictor variables found in logistic regression models of evening bat roost site selection on the natural site.

Level	Variable	Estimate	SE	Odds ratio	Σw_i
TREE	hardwood (- pine)	-0.2510	0.353	0.77800	1.0000
	dbh	0.0480	0.018	1.04914	1.0000
	height	0.0650	0.068	1.06711	1.0000
	live	-2.4817	0.684	0.08360	1.0000
PLOT	ov_height	-0.1708	0.080	0.84302	0.9996
	ov_dbh	0.0247	0.022	1.02497	0.9996
	ov_distance	-0.2720	0.078	0.76184	0.9996
	ov_pine	0.8700	0.934	2.38694	0.9996
	mid_height	-0.0257	0.074	0.97466	0.9996
	mid_distance	0.1044	0.075	1.11001	0.9996
	ov_nearest	0.0234	0.077	1.02363	0.9996
	STAND	open	0.0041	0.003	1.00410
	closed pine	-0.0005	0.000	0.99950	0.5745
	mature pine	-0.0224	0.009	0.97783	0.5745
	hardwood	-1.20E-05	0.003	0.99999	0.5745
	edge	-0.0025	0.007	0.99747	0.5745
	water	-0.0018	0.001	0.99823	0.5745
	stand size	-3.46E-07	8.76E-07	1.00000	0.5745
BUFF430	open	1.63E-05	5.88E-06	1.00002	0.7670
	closed pine	5.39E-06	1.36E-05	1.00001	0.7670
	hardwood	1.23E-05	5.74E-06	1.00001	0.7670
	mature pine	1.32E-05	4.88E-06	1.00001	0.7670