

BAT ACTIVITY AND ROOST-SITE SELECTION ON AN INTENSIVELY MANAGED
PINE LANDSCAPE WITH FORESTED CORRIDORS IN THE LOWER COASTAL PLAIN
OF SOUTH CAROLINA

by

CRIS DANIEL HEIN

(Under the Direction of Steven B. Castleberry and Karl V. Miller)

ABSTRACT

I used ultrasonic acoustic detectors and radiotelemetry to investigate relationships between bats and forested corridors on an intensively managed landscape in the Lower Coastal Plain of South Carolina. I modeled bat activity and roost-site selection with logistic regression and used Akaike's Information Criteria for small samples (AIC_c) to evaluate and select the most parsimonious model or set of models. Using Anabat II detectors, I recorded 16,235 bat echolocation call sequences from 320 sites along 32 pairs of corridor systems. I compared models relating occupancy of 6 bat species to site-level characteristics. My results indicated higher occupancy rates for all species along edge compared to interior corridor or adjacent stands. Although I found few differences among species with respect to site-level characteristics, bat activity was positively related with corridor overstory height and negatively related to adjacent stand age. Using radiotelemetry, I tracked 53 adult evening bats (*Nycticeius humeralis*) to 75 summer roosts. Evening bats roosted in a variety of structures, including cavities in hardwood trees and fork-topped loblolly pines (*Pinus taeda*). Approximately 40% of male and 20% of female roosts were located in corridor stands. Both male and female evening

bats tended to select roost-sites in mixed-pine hardwood stands. I also radiotracked 27 adult Seminole (*Lasiurus seminolus*) bats to 90 summer roosts. Seminole bats roosted exclusively in the canopy of live loblolly pines. Over 60% of both male and female roosts were located in corridor stands. Proximity to edge was negatively related to both male and female Seminole bats. I tracked 20 male Seminole bats to 71 winter roosts of varying structures, including pine needle clusters and leaf litter. On warmer nights, male Seminole bats selected taller trees in mature forest stands, but when minimum nightly temperatures were $<4^{\circ}\text{C}$, bats typically roosted on or near the forest floor in mid-rotation stands. Although I found similarities with respect to bat activity along corridor systems, roost-site selection differed between sex, species and season. Overall, results suggest a positive response by bats to forested corridors on an intensively managed pine landscape.

INDEX WORDS: AIC, Anabat, corridors, evening bat, forest management, *Lasiurus seminolus*, *Nycticeius humeralis*, radiotelemetry, roost-site selection, Seminole bat, South Carolina

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CRIS DANIEL HEIN

B.A., Texas A&M University, 1996

M.S., Texas State University, 2001

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CRIS DANIEL HEIN

Major Professor: Steven B. Castleberry
Karl V. Miller

Committee: Robert Cooper
James T. Peterson
T. Bently Wigley

Electronic Version Approved:

Maureen Grasso
Dean of the Graduate School
The University of Georgia
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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

Despite the diversity, distribution and ecological importance of bats, drastic reductions in many populations have occurred throughout the world, including North America (Pierson 1998). Of the 18 bat species in the southeastern United States, 87% carry special conservation status somewhere within their regional distribution (Laerm et al. 2000). As primary predators of night-flying insects, many of which are forest and agricultural pests, bats are vital components of forest ecosystems. In addition, because of their size, mobility, reproductive biology, and longevity, bats are good indicators of environmental quality (Altringham 1996, Kunz and Fenton 2003), and therefore should be considered in forest management decisions (Crampton and Barclay 1998). However, information regarding basic ecology and behavior, including details of roost selection, foraging areas, and population demographics, is lacking for most bat species (Fenton 2003; Miller et al. 2003).

Forests provide bats habitat for commuting and foraging, day and night roosts, summer maternity colonies, and winter hibernacula (Fenton 1997). Bats use trees for protection from predators, shelter from weather, and sites for social interactions (Morrison 1980, Fenton 1983, Vaughan et al. 1997). Among mammals of their size, bats are unique in having long lives, low reproductive rates, and relatively long periods of infant dependency (Findley 1993). This

combination of characteristics places them at risk of population decline in the presence of habitat disturbance (Soule 1986). Because availability of suitable habitat may be a limiting factor to bat populations (Fenton 1997), alterations in forest structure and composition can profoundly affect bat communities (Erickson and West 1996, Grindal 1998).

The area covered by industrial forests in the southeastern United States is expected to remain relatively constant for the next 20 years (National Commission on Science for Sustainable Forestry 2005). As a result, existing forest lands may shift to more intensively managed plantation systems to more efficiently and economically produce timber products (Wear and Greis 2002). Increased intensity of forest management in some locations often results in shorter harvest rotations, loss of late successional pine forests, and declines in species diversity of local vegetation communities (Allen et al. 1996). Efforts to minimize adverse impacts on local wildlife populations include such strategies as retention of forested corridors. The creation and maintenance of corridors in managed landscapes may represent an economically feasible and ecologically sound method for mitigating habitat loss resulting from timber harvests by providing suitable roosting and foraging opportunities for forest-dwelling bats. However, the utility of these linear landscape features as a management tool for bats is unclear.

Habitat selection by forest bats may be driven by the interaction between foraging and roosting requirements (Kunz 1982, Fenton 1990). Foraging activity may be greater near some stands because of proximity to favorable roosting habitat (Kunz 1982, Furlonger et al. 1987), thereby minimizing commuting flight distance and optimizing energy intake (Grindal and Brigham 1999). Thus, it is necessary to examine both habitat use and roost-site selection simultaneously. This study investigates the influence of forested corridors on bat activity and

roost-site selection on an intensively managed pine landscape in South Carolina. Furthermore, because little is known regarding the winter ecology of forest bats, I also examined winter roost-site selection by Seminole (*Lasiurus seminolus*) bats.

LITERATURE REVIEW

At least 9 of the 18 bat species that occur in the southeastern United States use forests for day-roosts and all 18 rely on forests for foraging habitat (Hall 1981). Of the 12 species occurring in the Lower Coastal Plain of South Carolina, 5 (42%) are listed as “Endangered” (e.g. *Corynorhinus rafinesquii*), “Threatened” (e.g. *Myotis austroriparius*), or as “Species of Concern” (e.g. *L. cinereus*, *L. intermedius* and *M. lucifugus*) (South Carolina Department of Natural Resources 2001). Several studies have examined the ecology of bats on intensively managed pine (*Pinus*) forests in this region (Menzel et al. 2002, Elmore et al. 2004, 2005, Menzel et al. 2005, Miles et al. 2006). However, information regarding methods for maintaining bat habitat in intensively managed landscapes is lacking (Wigley et al. 2007). Furthermore, virtually no data are available regarding seasonal changes in roost-site selection by bats in southern pine forests.

Bat Activity and Forested Corridors

The use of forested corridors in conservation strategies has been in practice for nearly 30 years (Wilson and Willis 1975). The retention of linear strips of vegetation in intensively managed forest systems may contribute to landscape heterogeneity and ecosystem maintenance, both critical components in sustainable resource management (Franklin and Forman 1987). Corridors are often designed to help conserve native flora and fauna, provide wildlife habitat, protect water quality, enhance aesthetics, and facilitate wildlife movement (Hobbs 1992).

To bats, linear landscape elements (i.e., corridors, hedgerows, tree lines, etc.) may provide sources of insect prey, navigational references, and shelter from wind and predators (Limpens and Kapteyn 1991, Verboom and Huitema 1997). Insect abundance and diversity may be greater along forest edges than in open areas or within interior forests (Lewis 1970), allowing bats foraging near these areas to maximize returns from foraging efforts (Verboom and Huitema 1997, Grindal and Brigham 1999). However, in cases where insect abundance is greater in interior forests or in open areas, bats continue to stay near edges, suggesting other advantages of forest-edge habitat in addition to food availability (Estrada et al. 1993, Grindal and Brigham 1999).

Linear features often facilitate commutes by bats from roost sites to foraging areas (Racey and Swift 1985, Limpens and Kapteyn 1991; Murray and Kurta 2004). Field studies and observations in The Netherlands over 2 decades indicate that most bat species select flyways along linear landscape elements instead of crossing open areas (Limpens and Kapteyn 1991, Verboom and Huitema 1997, Verboom and Spoelstra 1999, Verboom et al. 1999). In Britain, Walsh and Harris (1996) reported bats using linear features across a range of land classes and ownerships. Estrada and Coates-Estrada (2001) showed that live fence and vegetated stream corridors provided connectivity for bats of varying sizes, gender, age-classes, and feeding guilds across a fragmented landscape in Mexico. Because the use of corridors in intensively managed southern pine forests is a relatively new concept, the utility of these landscape features as a management tool for bats is unclear.

Summer Roost-site Selection

Roost sites are a critical resource for forest bats. Because bats spend over half of their time in diurnal roosts, the availability of suitable roosts is important in determining bat

population size and distributions (Kunz 1982). A recent synthesis of summer roosting studies indicated that bats typically select larger trees in areas with more open canopies (Kalcounis-Rüppel et al. 2005). The use of taller, more exposed roosts by bats likely increases solar exposure aiding prenatal and juvenile bat growth (Racey and Swift 1981, Racey 1988). Higher roosts also may be easier to access and relocate, and offer greater protection from predators (Vonhof and Barclay 1996).

Previous roost selection studies provided useful information regarding small-scale (i.e., tree and plot) characteristics of bat roosts (Miller et al. 2003, Kalcounis et al. 2005). However, bats may respond more to stand- and landscape-level attributes (Cryan et al. 2001, Elmore et al. 2004, Lunney et al. 1988, Miles et al. 2006). Roost locations may depend on proximity of other potentially limiting landscape features, such as water resources and foraging areas (Waldien et al. 2000). Furthermore, tree-roosting bats typically exhibit high fidelity to specific sites by roosting in different trees within a small area (Cryan et al. 2001, Elmore et al. 2004, Lunney et al. 1988), suggesting landscape-level features may have a greater influence on roosting area than specific roost structures (Miller et al. 2003).

Evening (*Nycticeius humeralis*) and Seminole bats are common forest-dwelling species found throughout the southeastern United States. Although each species uses trees for diurnal roosts, they exhibit different roosting strategies. Evening bats typically roost in tree cavities or under exfoliating bark (Jennings 1958, Chapman and Chapman 1990, Menzel et al. 1999, 2000, Miles et al. 2006). In contrast, Seminole bats typically roost in the canopy of live pine trees (Menzel et al. 1998, 1999, 2000, Perry and Thill 2007). Numerous small-scale studies have indicated the importance of tree- and plot-level features for both species. Evening bats typically select larger trees surrounded by a shorter, more open canopy compared to random sites (Menzel

et al. 1999, 2000, Miles et al. 2006). For Seminole bats, tree height, diameter at breast height (DBH), structure height above the canopy, and overstory basal area appear to be important factors in roost selection (Menzel et al. 1998, 2000, Perry and Thill 2007).

Evidence suggests that roost-site selection in both species may be influenced by large-scale habitat characteristics. Miles et al. (2006) concluded that evening bats select roost sites differently based landscape conditions (e.g., managed versus natural pine forests). The combination of low roost fidelity and high site fidelity in Seminole bats (Menzel et al. 2000, Perry and Thill 2007) indicates stand and landscape features may be more influential to roost-site selection compared to tree and plot characteristics (Cryan et al. 2001, Elmore et al. 2004, Lunney et al. 1988). Information supporting the effect of large-scale features on roost-site selection by evening and Seminole bats is lacking. Furthermore, no studies have examined the relationship between corridors and roost-site selection.

Winter Roost-site Selection

In temperate regions, winter research can be problematic due to low levels of bat activity (Hayes 1997). Winter activity levels decrease as many bat species migrate to warmer latitudes or hibernate in caves, crevices, or human-made structures (Fleming and Eby 2003, Speakman and Thomas 2003). As a result, forest and wildlife managers have relied on summer data to create year-round management strategies for forest bat populations. The paucity of information regarding winter roost-site selection suggests seasonal shifts in roosting behavior are not incorporated in existing management plans.

Understanding how seasonal changes affect roost-site selection is essential to effectively manage forest bat communities. Roosts are a fundamental aspect of bat ecology, providing suitable thermoregulatory conditions (Vaughan 1987). However, few studies have investigated

seasonal changes in roost-site selection. Recently, Miller et al. (2003) and Kalcounis-Rüegg et al. (2005) synthesized over two decades of research concerning summer roost-site characteristics. Although the numerous studies cited in these reviews provide insight into summer roosting habits of bats, their level of inference is limited to one season.

Seasonal changes in roost-site selection have been reported for tree-roosting bats. Boyles and Robbins (2006) reported tree- and plot-level differences in evening bat roosts between seasons. Indiana bats (*M. sodalis*) select snags as summer roosts, but hibernate in caves and mines during winter (Kurta and Rice 2002). In summer, southeastern foliage-roosting species such as Seminole and red (*L. borealis*) bats typically roost in the canopy of overstory trees (Menzel et al. 1998, 2000, Hutchinson and Lacki 2000, Elmore et al. 2004, Perry and Thill 2007, Hein et al. in press). However, these species appear to select alternate roosts in other seasons. Forest managers conducting winter burns have observed red bats flying from ground roosts in response to advancing prescribed fires (Saugey et al. 1989) and several authors have since reported the use of leaf litter by lasiurine bats (Saugey et al. 1998, Moorman et al. 1999, Rodrigue et al. 2001, Hein et al. 2005, Mormann and Robbins 2007). Roosting under leaf litter likely provides thermal benefits during extreme winter weather by reducing heat loss through convection and radiation (Whitaker and Stauffer 2003).

The use of leaf litter in winter suggests that prescribed fire, a common forest/wildlife management technique in southern pine forests, at this time may adversely affect bat populations. Many bat species have a low tolerance for roost disturbance. When disturbed, hibernating bats arouse and often abandon their roosts, expending critical winter stores of fat (Trani 2002). Furthermore, prescribed fires may destroy potential roost-sites and result in direct mortality of torpid bats roosting on the ground (Harvey and Saugey 2001). Despite numerous

reports of bats winter roosting on the ground, it is still unclear how frequently and under what conditions leaf litter roosts are used by lasiurine bats.

Forest Management and the MeadWestvaco Corporation

Southern forests are undergoing unprecedented landscape change caused by rapid growth in human population and subsequent urban expansion (Wear and Greis 2002). Because the area covered by industrial forests in the southeastern United States is expected to remain relatively constant for the next 20 years (National Commission on Science for Sustainable Forestry 2005), forest managers may shift to more intensively managed plantation systems to meet rising demands for forest products (Wear and Greis 2002). Increased intensity of forest management in some locations often results in even-aged systems with short harvest rotations limiting the availability of large snags and mature trees often used by forest-roosting bats (Allen et al. 1996, Wigley et al. 2007). Because intensive forest management will continue, it is important to gather information on habitat requirements for bat species to assess, predict and mitigate resulting impacts (Grindal and Brigham 1999).

The southeastern United States, particularly the Coastal Plain, contains a high proportion of intensively managed forests (Wear and Greis 2002). Several studies have evaluated the response by bats to various harvesting strategies in the region (Elmore et al. 2004, 2005, Menzel et al. 2002, 2005, Miles et al. 2006). However, information regarding methods for maintaining bat habitat on intensively managed landscapes is lacking (Wigley et al. 2007). Companies under sustainable forestry programs are expected to provide landscape-level habitat diversity to balance sustainable economic value and ecological objectives (Wigley et al. 2007). The MeadWestvaco Corporation, as a participant in the Sustainable Forestry Initiative (SFI), is committed to enhancing wildlife habitats through sustainable forest management (Sustainable Forestry

Initiative 2002). In 1992, the MeadWestvaco Corporation adopted a sustainable forestry management program on its South Region known as Ecosystem-Based Forestry. This program used a mixture of management zones (e.g. corridors) to maintain a diversity of forest structure and composition across the landscape (Constantine 2005).

I conducted my research on MeadWestvaco Corporation's South Region in southern South Carolina, USA. The area encompasses portions of Charleston, Colleton, and Dorchester Counties and is located in the Lower Coastal Plain physiographic province. The 41,365 ha area is intensively managed for loblolly pine (*P. taeda*) wood and fiber products and consists of even-aged stands in various successional stages. Plantation stands typically are clearcut at approximately 20–25 years of age. Silvicultural practices include mechanical and chemical site preparation and planting of cleared stands, 1 or 2 commercial thinnings, and vegetation management via prescribed fire. Twenty-five percent of the area is comprised of open stands (≤ 5 years), 15% is closed (6–11 years), and 33% is mid-rotation (12–22 years). Mature forest stands (≥ 23 years) include pine (6%), mixed pine-hardwood (10%), and hardwood (8%).

At the time of my study, The MeadWestvaco Corporation's Ecosystem-Based Forestry approach maintained a system of approximately 100–200 m wide corridors comprised of mature forests within a mosaic of younger plantation stands. Three types of corridors were retained in harvested areas: visual corridors maintained along public roads to enhance aesthetic quality, water quality corridors designed to protect wet areas and reduce soil erosion, and habitat diversity corridors intended to provide connectivity among non-timber zones, and enhance biodiversity and wildlife habitat. Forested corridors composed of mature pine, mixed pine-hardwood, or hardwood habitat constituted 11% of the total study area. Because these corridors contain older trees and greater complexity in structure and composition compared to surrounding

stands, bats may select these areas as potential roosting and foraging sites. Determining relationships between bats and forested corridors will assist forest and wildlife managers in developing guidelines that integrate habitat features beneficial to bats with forest management objectives.

OBJECTIVES AND GUIDE TO THE DISSERTATION

Forested corridors have been used in conservation strategies for decades (Wilson and Willis 1975). However, the influence of linear landscape features on bats, particularly with respect to roost-site selection, is unclear. The goal of this project was to investigate the potential of forested corridors to provide suitable habitat for forest-dwelling bats.

The dissertation is organized as a series of manuscript-style chapters addressing aspects of the study objectives described above. Chapter 2 examines site occupancy of 6 bat species at habitat diversity and water quality corridors. Using ultrasonic acoustical detectors, I recorded bat echolocation call sequences in corridor stands, along corridor edges, and in adjacent stands. I modeled species occupancy with site-level characteristics. This manuscript will be submitted to *Forest Ecology and Management*.

Chapters 3 and 4 address summer roost-site selection by cavity-roosting evening and foliage-roosting Seminole bats, respectively. I used radiotelemetry to locate individual diurnal roosts and modeled site-selection at the landscape scale. I examined the effect of forested corridors on summer roost-site selection and assessed differences in roosting behavior between sexes. The manuscript based on chapter 3 will be submitted to the *Journal of Wildlife Management*. The manuscript based on chapter 4 has been accepted by the *Journal of Mammalogy* and is currently in press.

In chapter 5, I investigated winter roost-site selection by Seminole bats. Using radiotelemetry, I examined differences in roosting strategies of Seminole bats between summer and winter. I also determined the influence of temperature on winter roost-site selection. This manuscript has been submitted to the *Journal of Wildlife Management*.

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CHAPTER 2

SITE-OCCUPANCY OF BATS IN RELATION TO FORESTED CORRIDORS¹

¹Hein, C.D., Miller, K.V., Castleberry, S.B. To be submitted to *Forest Ecology and Management*.

ABSTRACT

Forested corridors may be used to conserve native habitat, protect water quality, enhance aesthetics, and facilitate wildlife movement. While use of corridors by some wildlife species has been extensively examined, use of these landscape features by bats is poorly understood. From 1 June to 31 August 2004 and 2005, we used Anabat II detectors to examine bat activity and occupancy relative to forested corridors on an intensively managed forest landscape in southern South Carolina, USA. We compared bat activity among corridor interior, corridor edge, and stands adjacent to corridors. We also compared models relating occupancy of bat species to site-level characteristics using an information theoretic approach. We identified 16,235 call sequences of 8 species and detected bat presence at 89% (n = 320) of sites sampled. Our results indicate higher occupancy rates for bats along corridor edges compared to interior corridor or adjacent stands. Although we found few differences among species with respect to site-level characteristics, bat use was positively associated with corridor overstory height and negatively associated with adjacent stand age for all species. The presence of roads adjacent to corridor stands positively influenced occupancy of *Eptesicus fuscus*, *Lasiurus seminolus*, and *Peromyotis subflavus*. Our results suggest management practices designed to create and enhance corridors may represent an ecologically sound method for maintaining important bat habitat features (i.e., edge) across managed forest landscapes.

KEY WORDS Anabat; bats; corridors; forest management; pine plantation; South Carolina

INTRODUCTION

The southeastern United States is undergoing unprecedented landscape change caused by rapid growth in human population and subsequent urban expansion (Wear and Greis, 2002). Although the area covered by industrial forests in the southeastern United States is expected to remain relatively constant for the next 20 years (National Commission on Science for Sustainable Forestry 2005), habitat alteration may continue if existing forest lands shift to more intensively managed plantation systems to produce timber products more efficiently and economically (Wear and Greis, 2002). Increased intensity of forest management often results in shorter harvest rotations, loss of late-successional forests, and declining species diversity in local vegetation communities (Allen et al., 1996).

The creation of forested corridors has been suggested as an approach to maintain forest heterogeneity across fragmented landscapes. Juxtaposition of late-successional corridors within a mosaic of younger forests may help to conserve native flora and fauna, provide wildlife habitat, protect water quality, enhance aesthetics, and facilitate wildlife movement (Hobbs 1992). For bats, linear landscape elements may provide sources of insect prey, navigational references, protection from wind and predators, and roost sites (Limpens and Kapteyn 1991; Verboom and Huitema 1997; Estrada and Coates-Estrada, 2001; Hein, 2008; Hein et al., in press).

Previous studies have identified positive relationships between bats and linear landscape features (i.e., tree lines, hedgerows, streamside management zones, forested corridors). Field studies in The Netherlands over 2 decades indicate that most bat species select flyways along linear landscape elements instead of crossing open areas (Limpens and Kapteyn 1991; Verboom and Huitema, 1997; Verboom and Spoelstra, 1999; Verboom et al., 1999). In Britain, Walsh and Harris (1996) similarly reported bats using linear features across a range of land classes and

ownerships. Live fence and vegetated stream corridors provided connectivity for commuting and foraging bats to isolated forest patches in Mexico (Estrada and Coates-Estrada, 2001). In the southeastern United States, concurrent studies by Hein (2008) documented the selection of corridors as roost-sites for both cavity- and foliage-roosting bats. However, the influence of forested corridors on bat activity in this region is still unknown.

Our understanding of how bats respond to various forest management practices in the southeastern United States is limited (Menzel et al., 2002; Elmore et al., 2005; Miles 2006). Miller et al. (2003) recommended conducting research across an array of forest landscapes to examine impacts of different harvest strategies on bat populations. Our goal was to investigate the relationship between bats and forested corridors in an intensively managed landscape. Because corridors are relatively narrow features, bat activity is likely impacted by adjacent stands, nearby roads, and distance to water. Therefore, we also examined the influence of site-level characteristics to determine which corridors provided suitable habitat for bats. Based on echomorphology of bat species (Aldridge and Rautenbach, 1987), we predicted occupancy to be higher in open habitat (i.e., open-canopy adjacent stands) for low-frequency, less maneuverable bats, higher in forested corridors for high-frequency, more maneuverable bats, and higher for all bats along edge. Because bats often follow linear elements (Limpens and Kapteyn, 1991; Walsh and Harris, 1996; Grindal and Brigham, 1999), management practices designed to create and enhance corridors may offer increased opportunities to enhance habitat for forest bats.

METHODS

Study Area

We conducted our study on MeadWestvaco Corporation's South Region in southern South Carolina, USA. The area is located in the Lower Coastal Plain physiographic province

and is characterized by flat topography (slopes <2%) and elevations ranging from 20–30 m above mean sea level. Summers are warm and humid with monthly temperatures and precipitation averaging 27° C and 186 mm, respectively (NOAA-National Climatic Data Center, <http://www.ncdc.noaa.gov>).

The 41,365 ha study area is intensively managed for loblolly pine (*Pinus taeda*) wood and fiber products and consists of even-aged stands in various successional stages. Plantation stands typically are clearcut at approximately 20–25 years of age. Silvicultural practices include chemical and mechanical site preparation and planting of cleared stands, 1 or 2 commercial thinnings, and vegetation management via prescribed fire. Approximately 25% of the area is comprised of young stands and regeneration areas (≤ 5 years), 15% is closed (6–11 years), and 33% is mid-rotation (12–22 years). Mature forest stands (≥ 23 years) include pine (6%), mixed pine-hardwood (10%), and hardwood (8%). At the time of our study, MeadWestvaco employed a forest management system, known as Ecosystem-Based Forestry designed to increase diversity of forest structure and composition across the landscape (Constantine et al., 2005). This approach maintained a system of approximately 100–200 m wide corridors comprised of mature forests within a mosaic of younger plantation stands. Three types of corridors were retained in harvested areas: visual corridors situated along public roads, water quality corridors designed to protect wet areas and reduce soil erosion, and habitat diversity corridors intended to enhance biodiversity and wildlife habitat. Forested corridors composed of mature pine, mixed pine-hardwood, or hardwood habitat constituted 11% of the total study area.

Acoustic Detection and Analysis

From 1 June to 31 August in 2004 and 2005, we recorded bat echolocation sequences using Anabat II detectors (Titley Electronics, Ballina, New South Wales, Australia) coupled to Zero-

Crossing Analysis Interface Modules with CF memory card storage (Anabat CF Storage ZCAIM). We calibrated detectors to minimize variation in reception zones prior to field sampling (Larson and Hayes, 2000). Detector systems were housed in waterproof plastic containers and attached to tripods set at 1.5 m above the ground with the microphone oriented at a 45° angle (Weller and Zabel, 2002). We programmed detectors to begin recording 15 minutes prior to sunset and end 15 minutes after sunrise. We avoided sampling on nights with moderate to heavy rain.

We randomly selected one habitat diversity and one water quality corridor with similarly aged adjacent stands for simultaneous sampling for two consecutive nights. To increase the number of corridors sampled, we visited each pair of corridors once throughout the summer. We placed detector systems in the corridor interior, on each corridor edge, and in each adjacent stand for a total of 10 sample sites per night (5 detectors per corridor system x 2 corridor systems). To maximize independence of observations and reduce edge effects (Hunter, 1990), we positioned detectors in the center of each corridor and at least 40 m into adjacent stands (Grindal and Brigham, 1999). We oriented detectors in the corridor interior and on edges along corridor axes. Detectors set in adjacent stands were oriented away from the corridor. To maximize number of calls and standardize area sampled by detectors, we oriented detectors away from structural clutter (Grindal and Brigham, 1999; Weller and Zabel, 2002).

We analyzed echolocation sequences using Analook v4.9j software (Titley Electronics, Ballina, New South Wales, Australia). We used a customized filter to retain sequences of ≥ 5 calls and remove all recordings not consistent with properties of search-phase echolocation call sequences (Britzke and Murray, 2000). We also used Analook to calculate 10 parameter values for each call in a sequence (Britzke, 2003). We quantitatively identified each call sequence

using a discriminate function analysis (DFA) model based on an extensive call library of bats in the eastern United States (Britzke, 2003). We calculated percentage of call sequences correctly identified (accuracy rate) and percentage of sequences misidentified by species (Britzke 2003). Species identification can be difficult when multiple species possess similar search-phase call structures. However, accuracy rates increase for a single species at a site with the number of identified call sequences (Britzke et al., 2002). Therefore, we considered species with accuracy rates $\geq 80\%$ present at a site if ≥ 2 call sequences from that species were recorded. Species with accuracy rates $< 80\%$ were considered present if ≥ 4 call sequences were recorded. Hoary bats (*Lasiurus cinereus*), Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) and yellow bats (*Lasiurus intermedius*) were excluded from the DFA model prior to analysis. Hoary bats migrate through the region, but are not considered summer residents. Yellow bats are rarely encountered and Rafinesque's big-eared bats are difficult to detect acoustically with zero-crossing systems.

Habitat Metrics

At each survey site, we recorded stand type (corridor, edge, or adjacent stand), corridor type (habitat diversity or water quality), age of adjacent stands, and presence/absence of an adjacent road. We used ArcView 3.2 (ESRI, 2000) to measure distance (km) from each site to the nearest available water source (pond, river, drainage ditch). For each corridor, we used the point-centered-quarter method to determine basal area (BA), and mean height of overstory (≥ 10 cm) and midstory (3–10 cm) trees (Cottam and Curtis, 1956).

Model Selection

We considered each night a sampling visit. We considered a species present at a site if ≥ 2 or ≥ 4 call sequences were recorded during a sampling visit for species with accuracy rates $\geq 80\%$ or $< 80\%$, respectively. If no identifiable call sequences were recorded, we considered that

species as not detected (Yates and Muzika, 2006). We analyzed the resulting detection history using the program PRESENCE to estimate the proportion of sites used (MacKenzie et al., 2002). We used Akaike's Information Criterion for small sample sizes (AIC_c) to compare 8 detection probability models for each species. Covariates for detectability included year, Julian date, and temperature. We recorded the median temperature from 3 randomly placed HOBO data loggers (Onset Computer Corp., Bourne, Massachusetts, USA) set 1.5 m above the ground in open habitat. For each species, we incorporated the most parsimonious model of detection into all occupancy models.

We fit a global logistic regression model using detection/non-detection as the binary response and 9 explanatory variables (Table 2.1). Prior to model analysis we conducted correlation tests to ensure no pairs of variables were highly correlated (Spearman's $r > 0.7$). In addition to our global model, we selected 19 of a possible 511 candidate models based on our hypotheses relating bat species occupancy at corridor survey sites. We used the same set of candidate models for all bat species. We examined the temporal autocorrelation of our data by conducting an analysis of variance of the residuals from the global model for each species, using year as our independent variable. Our results indicated no temporal autocorrelation. Therefore, we conducted our analysis using traditional logistic regression techniques (Sokal and Rohlf 1995).

We assessed goodness-of-fit of our global model for each species using methods described by MacKenzie and Bailey (2004). Because our assessment indicated poor fit by the global model, we used the overdispersion factor ($\hat{c}$) to calculate $QAIC_c$. We calculated Akaike model weights (ω_i) to evaluate and select the most parsimonious model (Burnham and Anderson 2002). We established a confidence set by including models with Akaike weights within 10% of

the highest value (Royall 1997). We used model averaging to incorporate model selection uncertainty directly into parameter estimates and standard errors using Akaike weights. We based all inferences of parameter effects on this composite model. We calculated odds ratios (OR) from averaged parameter estimates. We evaluated ecological importance of each variable in the composite model by computing 90% confidence intervals for OR and interpreting the magnitude of the values within these intervals (Gerard et al. 1998).

RESULTS

We identified 16,235 call sequences from 32 pairs of corridors systems over two years. We detected bat presence at 89% ($n = 320$) sample sites. Six species were present at $\geq 15\%$ of sample sites and used for further analysis: 3,233 big brown bat (*Eptesicus fuscus*) sequences at 161 sites; 3,638 red bat (*Lasiurus borealis*) sequences at 117 sites; 2,972 Seminole bat (*L. seminolus*) sequences at 98 sites; 702 little brown bat (*M. lucifugus*) sequences at 76 sites; 1,610 evening bat (*Nycticeius humeralis*) sequences at 140 sites; and 1,736 eastern pipistrelle (*Peromyotis subflavus*) sequences at 122 sites. We also identified call sequences from silver-haired bats (*Lasionycteris noctivagans*, 359 sequences at 20 sites), Southeastern myotis (*Myotis austroriparius*, 968 sequences at 44 sites) and Mexican free-tailed bats (*Tadarida brasiliensis*, 1,017 sequences at 40 sites), but calls of those species occurred at $< 15\%$ of total sites sampled and were not included in analyses. We recorded more sequences along edges ($n = 13,884$, 54 call sequences/detector night) compared to adjacent stands ($n = 1,754$, 12 call sequences/detector night) and corridor interiors ($n = 1,581$, 7 call sequences/detector night).

Accuracy rates ranged from 100% to 33%, with 4 species $\geq 80\%$ and 5 species $< 80\%$ based on a single call sequence (Table 2.2). Accuracy rates increased to 98.5% for *E. fuscus*, 99.8% for *M. lucifugus*, and 96% for *N. humeralis* using 2 call sequences, and 89% for *L.*

borealis and 79% for *L. seminolus* using 4 call sequences. The DFA model commonly confused *M. austroriparius* calls with *M. lucifugus*. *Tadarida brasiliensis* calls were most commonly confused with *E. fuscus*. In contrast to many studies (Menzel et al., 2002; Ford et al., 2006), *L. borealis* and *L. seminolus* were not commonly mistaken for one another in our study and not combined into one species group.

We found no evidence of temporal autocorrelation between years and no correlation among covariates for species occurrence models. Our global model for species occupancy incorporated 9 site variables. Values of $\hat{c}$ for individual species global models were ≤ 4 suggesting no structural lack-of-fit (Burnham and Anderson 2002).

The most parsimonious model for detectability incorporated Julian date and was included in occupancy models for 4 species (*L. borealis*, *L. seminolus*, *M. lucifugus*, and *P. subflavus*). For these species, detectability increased from May to August. Temperature alone showed the most support for detecting *N. humeralis*, with increased detection negatively related to temperature. The detectability of *E. fuscus* was not influenced by any covariate or combination of covariates.

Three models predicting occurrence of *E. fuscus* were considered strongly competing with ΔQAIC_c values within 0.43 units (Table 2.3). These models were >2.6 times more likely than the next best approximating model. The confidence set included the top 4 models with a sum of Akaike weights of 0.92 indicating a 92% chance that one of these models was the best approximating model based on the data and set of candidate models. There was insufficient evidence to consider any additional models as plausible explanations for predicting *E. fuscus* occurrence. Edge and overstory height were included in all 4 models, and stand type and stand age were included in 3 of the 4 models from the confidence set. The composite model contained

5 covariates (stand type, edge, stand age, overstory height, and road) whose model-averaged 90% confidence intervals did not include zero, indicating they provided useful information in predicting *E. fuscus* occurrence (Table 2.4). Stand type, edge, overstory height and road were positively related, and stand age was negatively related to occurrence. Odds of *E. fuscus* occurrence were 27 times greater along edge and 5.8 times greater if a road was present.

The best approximating model for *L. borealis* incorporated stand type, edge, stand age, and overstory height with a 53% probability of being the best approximating model (Table 2.3). This model was 2.7 times more likely than the next best model. The confidence set included the top 4 models with a sum of Akaike weights of 0.86. Edge, stand age, and overstory height were included in all 3 models, and stand type was included in 2 of the 3 models from the confident set. The composite model contained 4 variables whose 90% confidence intervals did not include zero (stand type, edge stand age, and overstory height), all of which were positively related to occurrence except stand age (Table 2.4). Odds of *L. borealis* occurrence were 103 and 10 times greater along edge and in interior corridor stands, respectively.

The best approximating model for *L. seminolus* incorporated edge, stand age, and overstory height with a 39% probability of being the best approximating model (Table 2.3). This model was 1.5 and 2.7 times more likely than the next two models, respectively. The confidence set included the top 4 models with a sum of Akaike weights of 0.92. Edge and stand age were included in all 4 models, and stand type and overstory height were included in 3 of the 4 models from the confidence set. The composite model contained 5 variables whose 90% confidence intervals did not include zero (Table 2.4). Edge, overstory height, and road were positively related to occurrence, and stand type and stand age were negatively related. Odds of *L. seminolus* occurrence were Seminole bats were 28 and 5 times greater along edge and in adjacent

stands, respectively. Odds of *L. seminolus* occurrence were 5.3 times greater if a road was present.

The best approximating model for *M. lucifugus* incorporated stand type, edge, stand age, and overstory height with a 29% probability (Table 2.3). The confidence set included the top 6 models with a sum of Akaike weights of 0.84. Edge was the only covariate included in all 6 models. Stand type and age were included in 5, overstory height in 4, and corridor type in 3 models in the confidence set, respectively. The composite model contained 6 variables whose 90% confidence intervals did not include zero (Table 2.4). Stand type, edge, corridor type, and overstory height were positively related with occurrence, and stand age and distance to water were negatively related. Odds of *M. lucifugus* occurrence were 58 and 17 times greater along edge and in interior corridor stands, respectively, and 4 times greater in habitat diversity corridor systems.

The best approximating model for *N. humeralis* incorporated edge, stand age, and overstory height with a 37% probability (Table 2.3). This model was 1.8 and 3.6 times more likely than the next two approximating models, respectively. The confidence set included the top 4 models with a sum of Akaike weights of 0.78. Edge and stand age were included in all 4 models, and stand type and overstory height were included in 3 of the 4 models from the confidence set. The composite model contained 5 variables whose 90% confidence intervals did not include zero (stand type, edge, corridor type, stand age, and overstory height), all of which were positively related to occurrence except stand age (Table 2.4). Odds of *N. humeralis* occurrence were 9 times greater along edge.

Three models predicting occurrence of *P. subflavus* were considered strongly competing with ΔQAIC_c values within 0.78 units (Table 2.3). These models were >2.8 times more likely

than the next best approximating model. The confidence set included the top 4 models with a sum of Akaike weights of 0.77. Edge and stand age were included in all 4 models, and stand type and overstory height were included in 3 of the 4 models from the confident set. The composite model contained 5 variables whose 90% confidence intervals did not include zero (stand type, edge, stand age, overstory height, and road), all of which were positively related to occurrence except stand age (Table 2.4). Odds of *P. subflavus* occurrence were 66 times greater along edge and 8.6 times greater if a road was present.

DISCUSSION

Our findings are consistent with previous studies documenting the use of linear landscape features (i.e., vegetation and stream corridors, tree lines, and hedgerows) by commuting and foraging bats. Numerous studies in The Netherlands have documented a positive relationship between bats and linear elements (Limpens and Kapteyn, 1991; Verboom and Huitema, 1997; Verboom and Spoelstra, 1999; Verboom et al., 1999). In Britain, bats showed a positive selection for linear vegetation corridors, particularly those connecting favored foraging areas (Walsh and Harris, 1996). Estrada and Coates-Estrada (2001) showed that bats of varying sizes, gender, age-class, and feeding guilds used live fence and vegetation corridors in Mexico. They also noted that species richness increased along corridors closer to forested areas. Radiotagged Indiana bats (*M. sodalis*) also were observed following tree-lined paths in the northern United States (Murray and Kurta, 2004).

Linear landscape features may provide bats navigational references, commuting lanes, suitable foraging areas, and protection from wind and predators (Limpens and Kapteyn 1991; Verboom and Huitema, 1997). Kalko and Schnitler (1993) found that European pipistrelles (*Pipistrellus pipistrellus*) did not need landscape elements for acoustic landmarks. However,

Verboom et al. (1999) argued that bats may use linear features as landmarks without remaining in constant acoustical contact. Linear features often facilitate commutes from roost sites to foraging areas (Racey and Swift, 1985; Limpens and Kapteyn, 1991; Murray and Kurta, 2004). Small bats (i.e., *Myotis* spp.) travel farther distances along tree-lined paths, rather than flying directly to foraging areas by crossing open stands (Murray and Kurta, 2004). In addition, Racey and Swift (1985) found that foraging often occurred along flight routes. Because insects often accumulate on the lee side of linear features (Lewis, 1970), bat activity may correlate with increases in insect abundance (Furlonger et al., 1987; Limpens and Kapteyn, 1991). Activity by bats along the leeward side also suggests the importance of corridors as shelter from wind (Limpens and Kapteyn, 1991; Verboom and Spoelstra, 1999). Higher rates of bat activity also may be influenced by proximity to roost-sites (Barclay and Kurta, 2007; Carter and Menzel, 2007). Estrada and Coates-Estrada (2001) reported numerous roosting sites within large vegetation corridors bordering streams in Mexico. Hein (2008) found both cavity- and foliage-roosting bats selecting corridor stands as roost sites in the southeastern United States.

Bat occupancy was highest along corridor edges compared to interior corridor stands or adjacent stands in our study. Several studies have identified edge as an important habitat feature for bats. Walsh and Harris (1996) reported stronger selection for woodland edge than any other habitat type, including forest gaps. In Canada, activity was greatest along edge habitat compared to cutblocks or interior forest stands (Grindal and Brigham, 1999). Edge appears to be an important landscape component for free-flying bats because it provides low structural complexity and high insect abundance (Kalko and Schnitzler, 1993; Brigham et al., 1997). Kalko and Schnitzler (1993) suggested edge represents orderly and predictable clutter to bats flying parallel to edge. Several studies have shown higher activity levels in areas of low clutter

(Brigham et al., 1997; Humes et al., 1999; Sleep and Brigham, 2003). Although forests provide an important source of insect prey (Lewis, 1969; Kalcounis and Brigham, 1995; Grindal and Brigham, 1998), insect abundance and availability is often higher along forest edge (Lewis, 1970).

We found the probability of detection was positively related to Julian date for 4 bat species. Rising energetic demands imposed on pregnant and lactating female bats may account for increases in bat activity in early summer (Racey and Swift, 1985; Barclay, 1989). Activity may increase further in late summer as pups become volant (Seidman and Zabel, 2001). Yates and Muzika (2006) reported an increase in detection probability for pipistrelle bats for 4 weeks immediately following the onset of juvenile volancy. Evening bat detection was weakly related to cooler temperatures. This is inconsistent with previous studies showing a positive relationship between temperature and bat activity (Hayes, 1997; Yates and Muzika, 2006; Schirmacher et al., in press). Although temperature alone provided the most support for detecting evening bats, 90% confidence intervals from the composite model for this covariate included zero, suggesting temperature was not a useful predictor in our occupancy models. We did not include measures of vegetation density to determine detection probabilities. Patriquin et al. (2003) found that vegetation density did not affect the detectability of bats that echolocate near 40 kHz. Furthermore, they found that detecting bats echolocating near 25 kHz was easier in thinned conifer and mixed forests. Because corridors in our study were comprised of mature pine or mixed pine-hardwood stands with previous thinnings, we believe the influence of vegetative clutter on detection was minimal.

For most species in our study, occupancy was positively related with corridor stands. Based on echomorphology of bats (i.e., body size, wing morphology, and echolocation call

structure), we expected smaller, highly maneuverable bats to use corridor stands and larger, less maneuverable bats to use adjacent stands (Aldridge and Rautenbach, 1987). Use of corridor stands by *M. lucifugus* was consistent with our predictions. These small-bodied bats are considered clutter-adapted species, exhibiting low wing-loading and high-frequency calls (Kalcounis and Brigham, 1995; Kalcounis et al., 1999; Patriquin and Barclay, 2003; Owen et al., 2004). Contrary to predictions, big brown bats showed a positive relationship with corridor stands. Although the echomorphology of this species (i.e., high wing-loading, low frequency calls) suggests it is better adapted for open habitats, evidence suggests big brown bats are generalized, opportunistic foragers (Brigham, 1991; Owen et al., 2004). It is also possible that detections of big brown bats originated from individuals flying above the forest canopy. Studies examining the vertical stratification of bat activity have reported high levels above the canopy, particularly for larger species (Kalcounis et al., 1999; Menzel et al. 2005). Because our detectors were placed 1.5 m above the ground, we were unable to determine if bats were flying above or below the canopy.

Only *L. seminolus* showed a negative relationship with corridor stands, suggesting greater use of adjacent stands by this species. A morphologically similar species, the red bat, showed a strong positive relationship with corridor stands. Previous studies have shown red bats associated with a wide range of habitat types including cluttered areas (Carter et al., 2004; Menzel et al., 2005; Schirmacher et al., in press). Use of different stand types for these two similar species may represent a form of resource partitioning (Carter et al., 2004).

Several studies have reported higher bat activity along riparian areas compared to upland sites (Zimmermann and Glanz, 2000; Estrada and Coates-Estrada, 2001; Menzel et al., 2002; Owen et al., 2004; Schirmacher et al., in press). In our study, corridor type had little influence

on use, except for *M. lucifugus* and *N. humeralis*. Occupancy for these species was positively related to habitat diversity corridors. Kunz (1982) suggested that habitat selection may be driven by the interaction between foraging and roosting requirements. Hein (2008) found >50% of *N. humeralis* corridor roosts in habitat diversity corridors. Although roost-site selection for *M. lucifugus* is unknown on our site, other studies suggest that proximity to hibernacula and day-roosts influenced activity of this species (Barclay, 1984; Furlonger et al., 1987).

Corridor overstory height, adjacent stand age, and road presence also were important variables in predicting occupancy of forest bats along corridors. Occupancy was positively associated with taller corridor overstory height. Limpens and Kapteyn (1991) and Verboom and Huitema (1997) also found a positive relationship between height of a linear landscape elements and bat passes. Walsh and Harris (1996) noted that bats avoided stone walls without vegetation cover and low-cut hedges. Higher occupancy rates also were associated with younger, open (0–5 years) stands adjacent to corridors. The combination of these two features likely increased the effective overstory height and visibility of edge, making these corridors more suitable for free-flying bats. Furthermore, many bats, particularly larger species, forage over or near recently cleared stands (Verboom and Huitema, 1997; Grindal and Brigham, 1999; Patriquin and Barclay, 2003; Owen et al., 2004). We found the presence of roads adjacent to corridors positively influenced use for *E. fuscus*, *L. seminolus*, and *P. subflavus*. Use of roads is common for commuting and foraging bats (Krusic et al., 1996; Grindal and Brigham, 1998; Zimmerman and Glanz, 2000).

Determining species presence when multiple species in a community possess similar search-phase call structures is difficult (Britzke et al., 2002). Based on single call sequences, accuracy rates for 4 of 6 species we modeled were relatively high ($\geq 80\%$) while red (42%) and

Seminole (33%) bat accuracy rates were low in comparison. Because accuracy rates were based on single call sequences, these results represent minimum rates. As the number of sequences identified for a species increase at a site, so does the accuracy rate of identification, particularly if few calls of a similar species are recorded at that site (Britzke et al., 2002). As a result, the accuracy rate for red and Seminole bats approached 80% and 90%, respectively, when 4 calls were used to determine presence. Therefore, because we used ≥ 2 and ≥ 4 call sequences to determine presence of species with accuracy rates ≥ 80 and < 80 , respectively, we believe our models are representative of these species.

CONCLUSION

We found high rates of bat use associated with forested corridors. Bat activity and occupancy rates were higher along corridor edges compared to interior corridor or adjacent stands. Edge appears to be an important component for commuting and foraging bats and should be maintained across the landscape. Features associated with edge (e.g., adjacent stand age, corridor overstory height, and road presence) may enhance occupancy rates by forest bats. Forested corridors in managed landscapes may represent an ecologically sound method for maintaining important bat habitat features (i.e., edge). Use of forested corridors is a relatively new concept in intensively managed landscapes of the southeastern United States. Additional research is needed to demonstrate the effectiveness of corridors in providing suitable commuting and foraging habitat in different regions and landscape conditions.

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Table 2.1. Variables included in the global model relating bat species occupancy with corridor survey sites in southern South Carolina, June-August, 2004-2005.

Variable	Definition
Stand type (stand)	Categorical variable (1 = corridor interior, 0 = otherwise)
Edge (edge)	Categorical variable (1 = corridor edge, 0 = otherwise)
Corridor type (ctype)	Categorical variable (1 = habitat diversity, 0 = water quality)
Stand age (sage)	Age (years) of adjacent stand
Basal area (ba)	Density (m^2/ha) of trees in corridor stand
Overstory height (oht)	Average height (m) of overstory trees in corridor stand
Midstory height (mht)	Average height (m) of midstory trees in corridor stand
Road (rd)	Categorical variable (1 = road present, 0 = road absent)
Distance to water (dw)	Distance (km) to nearest water source (pond, drainage ditch, river)

Table 2.2. Percent classification rates based on a single call sequence for big brown bats (EPFU), red bats (LABO), Seminole bats (LASE), southeastern myotis (MYAU), little brown bats (MYLU), evening bats (NYHU), eastern pipistrelles (PESU), and Mexican free-tailed bats (TABR) recorded at corridor survey sites in southern South Carolina, June-August 2004-2005. Numbers in columns represent the percentage of calls identified as the corresponding species in each row.

	EPFU	LABO	LANO	LASE	MYAU	MYLU	NYHU	PESU	TABR
EPFU	87.8	—	11.1	—	—	—	—	—	50.0
LABO	—	42.0	—	—	12.5	—	12.0	—	—
LANO	10.4	—	66.7	—	—	—	—	—	—
LASE	—	8.0	—	33.3	—	—	8.0	—	—
MYAU	—	—	—	33.3	50.0	4.3	—	—	—
MYLU	—	2.0	—	—	25.0	95.7	—	—	—
NYHU	—	36.0	—	—	—	—	80.0	—	—
PESU	—	12.0	—	33.3	12.5	—	—	100.0	—
TABR	1.7	—	22.2	—	—	—	—	—	50.0

Table 2.3. Model selection results for the confidence set of models used to predict occupancy of 6 bat species at corridor survey sites in southern South Carolina, June-August, 2004-2005.

Variables defined in Table 1.

Model	K	QAICc	Δ QAIC	Weight
EPFU				
$\Psi(\text{stand edge sage oht}) p(.)$	6	240.14	0.00	0.3132
$\Psi(\text{edge sage oht}) p(.)$	5	240.56	0.42	0.2537
$\Psi(\text{stand edge sage oht rd}) p(.)$	7	240.57	0.43	0.2529
$\Psi(\text{stand edge ctype oht}) p(.)$	6	242.48	2.34	0.0972
LABO				
$\Psi(\text{stand edge sage oht}) p(\text{julian})$	7	135.99	0.00	0.5281
$\Psi(\text{stand edge sage oht rd}) p(\text{julian})$	8	137.95	1.96	0.1987
$\Psi(\text{edge sage oht}) p(\text{julian})$	6	138.70	2.71	0.1366
LASE				
$\Psi(\text{edge sage oht}) p(\text{julian})$	6	96.13	0.00	0.3895
$\Psi(\text{stand edge sage oht}) p(\text{julian})$	7	96.95	0.82	0.2595
$\Psi(\text{stand edge sage oht rd}) p(\text{julian})$	8	98.15	2.02	0.1419
$\Psi(\text{stand edge ctype sage}) p(\text{julian})$	7	98.41	2.28	0.1251
MYLU				
$\Psi(\text{stand edge sage oht}) p(\text{julian})$	7	113.59	0.00	0.2894
$\Psi(\text{stand edge ctype sage}) p(\text{julian})$	7	114.86	1.27	0.1531
$\Psi(\text{stand edge sage oht rd}) p(\text{julian})$	8	115.29	1.70	0.1236
$\Psi(\text{stand edge ctype oht}) p(\text{julian})$	7	115.45	1.86	0.1142
$\Psi(\text{stand edge ctype sage dw}) p(\text{julian})$	8	115.79	2.20	0.0961
$\Psi(\text{edge sage oht}) p(\text{julian})$	6	116.63	3.04	0.0633
NYHU				
$\Psi(\text{edge sage oht}) p(\text{temp})$	6	164.61	0.00	0.3744
$\Psi(\text{stand edge sage oht}) p(\text{temp})$	7	165.77	1.16	0.2094
$\Psi(\text{stand edge sage oht rd}) p(\text{temp})$	8	167.16	2.55	0.1046
$\Psi(\text{stand edge ctype sage}) p(\text{temp})$	7	167.38	2.77	0.0937
PISU				
$\Psi(\text{edge sage oht}) p(\text{julian})$	6	165.11	0.00	0.2696
$\Psi(\text{stand edge sage oht}) p(\text{julian})$	7	165.21	0.10	0.2560
$\Psi(\text{stand edge sage oht rd}) p(\text{julian})$	8	165.89	0.78	0.1829
$\Psi(\text{stand edge ctype sage}) p(\text{julian})$	7	167.95	2.84	0.0654

Table 2.4. Model-averaged estimates and odds ratios for 6 bat species at corridor survey sites in southern South Carolina, June-August, 2004-2005. Variables defined in Table 1.

	Estimate (SE)	Lower 90% CI	Upper 90% CI	OR	Lower OR 90% CI	Upper OR 90% CI
EPFU						
Ψ(intercept)	-5.82 (1.12)	-7.66	-3.98			
stand	1.01 (0.40)	0.35	1.66	2.74	1.43	5.27
edge	3.28 (0.47)	2.51	4.06	26.71	12.32	57.88
ctype	-0.30 (0.33)	-0.84	0.25	0.74	0.43	1.28
sage	-0.15 (0.06)	-0.24	-0.05	0.86	0.79	0.95
oht	0.23 (0.08)	0.10	0.36	1.26	1.10	1.44
rd	1.76 (1.00)	0.12	3.40	5.80	1.26	29.91
p(intercept)	0.85 (0.04)	0.79	0.90			
LABO						
Ψ(intercept)	-6.83 (1.60)	-9.46	-4.20			
stand	2.32 (0.58)	1.37	3.28	10.19	3.93	26.45
edge	4.64 (0.81)	3.31	5.97	103.55	27.43	390.93
sage	-0.41 (0.10)	-0.57	-0.24	0.66	0.56	0.79
oht	0.28 (0.07)	0.16	0.39	1.32	1.18	1.48
rd	0.66 (0.88)	-0.78	2.11	1.94	0.45	8.22
p(intercept)	-6.44 (0.26)	-6.87	-6.01			
julian	0.035 (0.001)	0.033	0.037	1.036	1.034	1.039
LASE						
Ψ(intercept)	-3.07 (1.72)	-5.89	-0.24			
stand	-1.59 (0.67)	-2.68	-0.48	0.20	0.07	0.61
edge	3.34 (0.59)	2.36	4.31	28.13	10.63	74.41
ctype	0.57 (0.41)	-0.10	1.25	1.77	0.90	3.48
sage	-0.50 (0.09)	-0.66	-0.35	0.60	0.52	0.70
oht	0.19 (0.06)	0.09	0.29	1.21	1.09	1.34
rd	1.67 (0.82)	0.31	3.02	5.30	1.37	20.49
p(intercept)	-12.54 (0.32)	-13.06	-12.02			
julian	0.067 (0.001)	0.065	0.069	1.068	1.066	1.071
Mylu						
Ψ(intercept)	-6.16 (2.99)	-11.06	-1.25			
stand	2.82 (0.74)	1.61	4.04	16.81	4.99	56.55
edge	4.06 (0.91)	2.57	5.55	57.96	13.01	258.20
ctype	1.43 (0.57)	0.48	2.37	4.16	1.62	10.65
sage	-0.37 (0.13)	-0.57	-0.16	0.69	0.56	0.85
oht	0.28 (0.08)	0.15	0.411	1.32	1.16	1.51
rd	1.09 (0.89)	-0.37	2.56	2.99	0.69	12.93
dw	-0.71 (0.36)	-1.3	-0.12	0.49	0.27	0.89
p(intercept)	-5.61 (0.32)	-6.14	-5.08			
julian	0.026 (0.002)	0.024	0.029	1.027	1.024	1.03

Table 2.4. Continued

Parameter	Estimate (SE)	Lower 90% CI	Upper 90% CI	OR	Lower OR 90% CI	Upper OR 90% CI
NYHU						
$\Psi(\text{intercept})$	-2.84 (1.20)	-4.81	-0.88			
stand	0.77 (0.40)	0.10	1.43	2.15	1.11	4.18
edge	2.19 (0.38)	1.57	2.82	8.98	4.79	16.82
ctype	0.54 (0.30)	0.05	1.03	1.71	1.05	2.80
sage	-0.28 (0.06)	-0.37	-0.18	0.76	0.69	0.84
oht	0.14 (0.05)	0.07	0.22	1.15	1.07	1.25
rd	1.14 (0.77)	-0.13	2.40	3.12	0.88	11.06
p(intercept)	4.19 (2.50)	0.08	8.30			
temp	-0.15 (0.11)	-0.33	0.02	0.86	0.72	1.02
PISU						
$\Psi(\text{intercept})$	-3.64 (1.61)	-6.28	-1.01			
stand	1.32 (0.54)	0.44	2.20	3.75	1.55	9.06
edge	4.19 (0.72)	3.01	5.37	66.14	20.31	215.4
ctype	0.003 (0.42)	-0.68	0.69	1.00	0.51	1.99
sage	-0.35 (0.09)	-0.50	-0.21	0.70	0.54	0.92
oht	0.18 (0.06)	0.07	0.28	1.19	1.08	1.32
rd	2.15 (1.06)	0.41	3.90	8.61	1.51	49.21
p(intercept)	-8.74 (0.27)	-9.18	-8.31			
julian	0.046 (0.004)	0.039	0.053	1.047	1.054	1.040

CHAPTER 3

SEX-SPECIFIC SUMMER ROOST-SITE SELECTION BY EVENING BATS ON A
MANAGED PINE LANDSCAPE WITH FORESTED CORRIDORS²

² Hein, C. D., S. B. Castleberry, and K. V. Miller. To be submitted to *The Journal of Wildlife Management*.

ABSTRACT

The creation and maintenance of forested corridors to increase landscape heterogeneity has been practiced for decades, but is a relatively new concept in intensively managed southern pine forests. To bats, linear landscape features may offer suitable foraging and roosting sites. We used radiotelemetry to investigate summer roost-site selection by evening bats (*Nycticeius humeralis*) in an intensively managed landscape with forested corridors in southern South Carolina, USA, 2003-2006. We tracked 53 (26 M, 27 F) adult evening bats to 75 (31 M, 44 F) diurnal roosts. Male bats roosted alone, primarily in tree cavities (77%), whereas females typically roosted colonially in tree cavities (56%) or fork-topped pine trees (34%). Male bats roosted in corridor stands more often (40%) compared to female bats (18%). We modeled roost-site selection with logistic regression and used Akaike's Information Criterion for small samples (AIC_c) and Akaike weights to select models relating roost-site selection to landscape-level features. Model selection results indicated the importance of older mixed pine-hardwood stands as roost sites for both male and female bats. The influence of other landscape features (i.e., distance to open and distance to mid-rotation stands) differed between males and females. Although evening bats primarily selected mature forest habitat as roost-sites, mid-rotation stands commonly found on intensively managed forests may offer alternative roosts (i.e., fork-topped pine trees) especially for reproductive females. Understanding sex-specific roost-site selection will further assist managers in developing guidelines to create and maintain habitat features beneficial to forest bats.

KEY WORDS AIC, bats, corridors, evening bat, *Nycticeius humeralis*, pine, *Pinus*, radiotelemetry, roost-site selection, South Carolina.

INTRODUCTION

The southeastern United States, particularly the Coastal Plain, contains a high proportion of intensively managed forests (Wear and Greis 2002). Industrial forest companies in the region often manage using even-aged systems with short rotations to meet demand for some forest products (Wigley et al. 2007). However, when rotations are short, the availability of large snags and older trees, often used by forest-roosting bats, can be limited (Allen et al. 1996). To balance sustainable economic value and ecological objectives, companies under sustainable forestry programs are expected to provide landscape-level habitat diversity (Wigley et al. 2007). One approach to maintaining a variety of forest structure and composition across managed landscapes is the retention of corridors comprised of late-successional forest habitat.

Forested corridors have been used in conservation strategies for decades (Wilson and Willis 1975). Corridors are often maintained to preserve native flora and fauna, protect water quality, enhance aesthetics, and facilitate wildlife movement (Hobbs 1992). Bats likely use linear landscape features such as corridors as navigational references, foraging areas, and protection from wind and predators (Limpens and Kapteyn 1991, Verboom and Huitema 1997, Estrada and Coates-Estrada 2001). Corridors comprised of mature forest also may provide structures (i.e., tall, large-diameter trees, snags) used as day-roosts by forest-dwelling bats. Hein et al. (in press) found foliage-roosting Seminole bats (*Lasiurus seminolus*) selecting forested corridors for summer roost-sites. However, the influence of forested corridors on roost-site selection by cavity-roosting bats remains unknown.

Evening bats (*Nycticeius humeralis*) are a common cavity-roosting species found throughout the southeastern United States (Watkins 1972). Previous summer studies have provided insight regarding small scale characteristics of evening bat tree roosts (Menzel et al.

1999, 2000, 2001, Boyles and Robbins 2006, Miles et al. 2006). Less well understood are large scale features affecting evening bat roost-site selection (but see Miles et al. 2006). Furthermore, information regarding differences in roost-site selection between sex and reproductive condition is limited. Our goal was to examine the influence of landscape-level features, including forested corridors, on evening bat roost-site selection, by sex and reproductive condition, within an intensively managed pine forest.

STUDY AREA

We conducted our research across a 41,365-ha study area owned by the MeadWestvaco Corporation in southern South Carolina, USA. The study area is located in the Lower Coastal Plain physiographic province and is characterized by flat topography (slopes <2%) and elevations ranging from 20–30 m above mean sea level. Summers are warm and humid with monthly temperatures and precipitation averaging 27° C and 18.6 cm, respectively (NOAA-National Climatic Data Center, <http://www.ncdc.noaa.gov>).

The area is intensively managed for loblolly pine (*Pinus taeda*) wood and fiber products and consists of even-aged stands in various successional stages. Plantation stands typically are clearcut at approximately 20–25 years of age. Silviculture includes site preparation and planting of cleared stands, 1 or 2 commercial thinnings, and vegetation management via fire, mechanical and, chemical treatments. At the time of our study, MeadWestvaco employed a unique forest management system, known as Ecosystem-Based Forestry, designed to increase heterogeneity of wildlife habitat (Constantine et al. 2005). This approach maintained a system of approximately 100–200 m wide corridors comprised of late-successional habitats creating diversity of forest structure and composition across the landscape. These forested corridors, composed of mature pine, mixed pine-hardwood, or hardwood habitat, constituted 11% of the total study area.

METHODS

We captured evening bats from late May through mid-August 2003–2006 using 2–4 mist-nets 6 m to 12 m in length set over 9 randomly selected ponds. Ponds were located in open areas, adjacent to roads, and distributed throughout the study area. We recorded mass (g), forearm length (mm), sex, reproductive condition (Racey 1988), and relative age (Anthony 1988) of captured bats. We attached 0.43-g (Biotrack, Wareham, Dorset, UK) or 0.33-g (Blackburn Transmitters, Nacogdoches, Texas, USA) radiotransmitters to the back of adult evening bats using Skin Bond surgical adhesive (Pfizer, Largo, Florida, USA). Transmitter load (males: mean = 3.6%, range = 2.5–4.9%; females: 2.9%, range = 1.9–3.8%) was <5% body mass (Aldridge and Brigham 1988). Bats were held for 20 minutes to allow adhesive to set and released at point of capture. We conducted bat capture and handling under University of Georgia Institutional Animal Care and Use Committee guidelines (IACUC # 2003-10029-ml).

We located day-roosts using telemetry receivers (TRX 2000S, Wildlife Materials, Inc., Murphysboro, Illinois, USA) and 3-element Yagi antennas. We tracked bats daily, when possible, beginning the day after capture until the transmitter failed or was recovered. We focused our tracking efforts on new bats or those with fewer identified roosts. We conducted evening emergence counts, when possible, to verify roost location and determine colony size within roosts. Counts began 30 min prior to sunset and continued until bats were no longer visible. We recorded roost locations using a Geoexplorer III or Geoexplorer XT (Trimble Navigation, Sunnyvale, California, USA) Global Positioning System (GPS) unit. Coordinates were differentially corrected using Pathfinder software (Trimble Navigation) and imported into a Geographic Information System (GIS) for analysis.

Habitat Sampling

To characterize structure- and plot-level features, we collected quantitative data for all roost structures (i.e., trees and snags) and an equal number of random structures (Table 3.1). For each roost structure, we selected a random structure similar to that used by the bat. To avoid overlap between roost and random structures and to ensure random structures were in the same forested stand, random structures were located 50–100 m from roosts in a random direction. We recorded species, diameter at breast height (DBH: 1.4 m from base of tree), and height of structure for all roost and random trees. We considered height to the lowest cavity as the “roost height” for each random structure. We established a 0.04-ha circular plot (radius = 11.35 m) centered on each roost and random tree and recorded species, DBH, and height of all overstory trees (DBH ≥ 10 cm). We measured all diameters and heights using a DBH tape (Spencer Products Co., Seattle, Washington, USA) and 400LH laser hypsometer (Opti-Logic Corp., Tullahoma, Tennessee, USA), respectively.

To examine stand- and landscape-level selection by evening bats, we defined 6 stand types: open, closed, mid-rotation, mature pine, mixed pine-hardwood, and hardwood. Open stands included clearcut and regenerating stands ≤ 5 years old, non-productive fields, and wildlife openings (i.e., food plots). Closed stands were dense, pre-thinned stands (6–11 years) with complete canopy closure. Mid-rotation stands were 12–22 years old with almost complete canopy closure. Silvicultural prescriptions (i.e., burning, thinning) often occurred in these stands creating a more open canopy. Mature pine stands consisted of upland pine ($>75\%$ pine basal area) stands ≥ 23 years old. Mixed pine-hardwood stands were mature stands (≥ 23 years) containing 25%–75% pine basal area located on poorly developed soils. Hardwood stands ($<25\%$ pine basal area) typically were >50 years old and associated with riparian zones or areas

of poorly drained soils. Approximately 25% of the study area consisted of open habitat, 15% was closed, 33% was mid-rotation, 6% was mature pine, 10% was pine-hardwood, and 8% was hardwood.

We determined the area of potentially available habitat based on observed evening bat ecology (Taylor 1999, Arnett 2007). We used ArcView 3.2 to create circular landscapes (males: radius = 2.5 km, area = 1,963 ha; females: radius = 3.5 km, area = 3,848 ha) around 9 capture ponds. These radii represented the maximum distances flown from capture pond to roost by male and female bats, respectively. Because water sources were limited or ephemeral, bats likely remained close to these ponds. All stand types were available in each landscape in relative proportion to the total study area.

We selected random sites from a grid of 250 points within each circular landscape. The number of random sites we selected in each landscape equaled the number of roost structures located per capture pond. We updated GIS layers each year with stand and landscape data to control for changes in availability of habitat types among years. We recorded stand age for all roost and random sites. We measured distance (m) from each roost and random site to nearest edge or road and to nearest corridor. We also measured distances (m) to nearest edge of each stand type. A value of zero was assigned to the stand type in which the roost or random site was found (Conner et al. 2003). Because we used the maximum distance traveled from capture pond to roost to define our available landscape, we did not include distance to water in our analysis.

Analysis and Model Development

We conducted correlation analysis to ensure no pairs of variables were highly correlated (Spearman's $r > 0.7$). Prior to model analysis, we separated our data by sex and further divided females into separate reproductive conditions, pregnant (PF), lactating (LF), and non-

reproductive (NF). We created a global logistic regression model, using 8 distance measures, to describe roost-site selection by evening bats. We tested our global model, using data from each sex and reproductive condition, for goodness-of-fit using the Hosmer-Lemeshow statistic. In addition to our global model, we selected 47 of a possible 255 candidate models based on our hypotheses relating roost-site selection to landscape variables. We used the same set of candidate models for both male and female bats. All variables appeared in an equal number of models creating a balanced model set.

Prior to model analysis, we examined the spatial and temporal autocorrelation of our data. We fit our global logistic regression model with structure type (roost vs. random) as the binary response and conducted an analysis of variance of the residuals using the bat or year as our independent variable (Rieman et al. 2006). Our results indicated no significant spatial or temporal autocorrelation. Because our data were independent, we conducted our analysis, with the roost as the experimental unit, using traditional logistic regression (Sokal and Rohlf 1995).

We used the log-likelihood for each model to calculate Akaike's Information Criterion for small sample sizes (AIC_c). We calculated Akaike model weights (ω_i) to evaluate and select the most parsimonious model and to predict variable importance (Burnham and Anderson 2002). We created a confidence set of models by including those models with Akaike weights within 10% of the highest value, which is comparable with the minimum cutoff point suggested by Royall (1997). We calculated Nagelkerke's R^2 for all models, to assess variation explained by each model contained within the confidence set (Nagelkerke 1991).

We used model averaging to incorporate model selection uncertainty directly into parameter estimates and standard errors using Akaike weights (Burnham and Anderson 2002). We calculated odds ratios (OR) from averaged parameter estimates. However, because larger or

smaller unit changes may be more ecologically interpretable, we calculated scaled OR when appropriate (Hosmer and Lemeshow 2000). We evaluated the ecological importance of each variable in the composite model by computing 90% confidence intervals for the scaled OR and interpreting the magnitude of the values within these intervals (Gerard et al. 1998).

We used leave-one-out cross validation as a means of determining the predictive power of our selected model (Neter et al. 1996). We used an estimated probability of presence ≥ 0.5 as the criterion for presence. All analyses were conducted using SAS version 8.0 (SAS Institute, 2001). We report values as means $\pm$ SE unless stated otherwise.

RESULTS

We radiotracked 26 adult male and 27 (7 PF, 15 LF, 5 NF) adult female evening bats to 31 and 44 (11 PF, 24 LF, 9 NF) individual roost trees, respectively. Evening bats roosted in 9 tree species including swamp tupelo (*Nyssa sylvatica biflora*), bald cypress (*Taxodium distichum*), water oak (*Quercus nigra*), sweetgum (*Liquidambar styraciflua*), Carolina ash (*Fraxinus caroliniana*), Hickory (*Carya* spp.), and American elm (*Ulmus americana*). But, loblolly pine (8 M, 7 PF, 6 LF, 2 NF) and red maple (*Acer rubrum*) (7 M, 1 PF, 8 LF, 2 NF) were the most commonly used species. Roost types included tree cavities (24 M, 4 PF, 14 LF, 7 NF), fork-topped loblolly pines (4 M, 7 PF, 8 LF), live trees (2 M, 2 LF, 1 NF), and exfoliating bark (1 M). Evening bats roosted in four different stand types, mid-rotation (6 M, 6 PF, 2 LF, 1 NF), mature pine (4 M, 1 PF, 6 LF, 2 NF), mixed pine-hardwood (13 M, 4 PF, 14 LF, 5 NF), and hardwood (8 M, 0 PF, 2 LF, 1 NF). Male evening bats (roosts = 12) selected corridor stands more often compared to female bats (roosts = 8: 2 PF, 4 LF, 2 NF).

Eighty-nine percent of males (mean = 0.81 km, range = 0.1–2.5 km) and 84% of females (mean = 1.2 km, range = 0.2–3.5 km) roosted ≤ 1.5 km from point of capture. Male bats always

roosted individually while females roosted alone or in colonies. Five trees were used by >1 radiotagged female. We located 33 maternity colonies, 15 in fork-topped trees and 18 in tree cavities. Colony size varied by structure type, with smaller colonies located in fork-topped trees (4–27 bats) and larger colonies in tree cavities (≥ 22 bats). Four cavity trees contained >50 bats, two of these had >100 bats. Male bats often remained in the same roost for the life of the transmitter. Female bats often switched roosts daily. However, transmitters typically were removed ≤ 3 days as a result of colonial grooming. Thus, we were unable to calculate roosting home ranges for male and female evening bats as few bats were tracked to ≥ 3 roosts.

Male bats typically selected shorter and smaller roost structures surrounded by higher basal area compared to random structures (Tables 3.2). In contrast, LF bats selected taller and larger trees as roosts. Both PF and LF bats roosted higher in trees compared to random structures. Similar to males, NF bats tended to roost in smaller trees compared to random structures. Pregnant and LF roosts typically were taller and larger than male and NF roosts. Male, LF and NF bats roosted in older-aged stands compared to random sites.

We developed models for male and LF bats. We did not create models for pregnant and NF bats due to insufficient sample sizes. Spearman tests showed no correlation among distance variables for male and LF bats. Our results indicated no significant spatial (males: $F_{25,36} = 0.35$, $P = 0.9965$; lactating females: $F_{14,33} = 0.7$, $P = 0.7606$) or temporal (males: $F_{3,58} = 0.32$, $P = 0.8106$; lactating females: $F_{3,44} = 0.53$, $P = 0.6620$) autocorrelation. Our global model incorporated distance to nearest corridor, distance to nearest edge or road, and distances to 6 stand types. The global model provided an adequate fit to the data for male (Hosmer-Lemshow GOF statistic₈ = 7.7707, $P = 0.4562$) and lactating female (Hosmer-Lemshow GOF statistic₈ = 4.9951, $P = 0.7581$) bats, respectively.

Roost-site Selection by Males

The best approximating model for roost-site selection by males incorporated distance to nearest corridor and distances to nearest open and mixed pine-hardwood stands with a 68.5% probability (Table 3.3). This model was 8.8 times more likely than the next best approximating model, which contained distances to nearest open and mixed pine-hardwood stands. The confidence set of models included the top 2 models with a sum of Akaike weights of 0.763 indicating a 76.3% chance that 1 of these models was the best approximating model based on the data and set of candidate models. There was insufficient evidence to consider the remaining models as plausible explanations for roost-site selection. Distance to nearest corridor and distance to nearest mixed pine-hardwood stand were negatively related, and distance to nearest open stand was positively related with site selection (Table 3.4). The other 5 distance measures had model averaged 90% confidence intervals that included zero, indicating they provided little information regarding roost-site selection. Distance to nearest mixed pine-hardwood stand had the highest importance value, followed by distance to nearest corridor and distance to nearest open stand. The composite model contained 3 variables whose scaled OR were relatively precise (90% confidence interval does not include 1: Table 3.5). Roost sites were 9% less likely to occur for every 25 m increase in distance to nearest mixed pine-hardwood stand and 9% more likely for every 25 m increase in distance to nearest open stand. The odds of a roost occurring decreased 8% for every 25 m increase in distance from nearest corridor. We evaluated model performance for male roost-site selection using the top model from our confidence set. The top model incorrectly predicted 18% of used sites as random and 24% of random sites as roosts. Based on our classification rates, our top model classified 75% of roosts and 84% of random sites correctly.

Roost-site Selection by Lactating Females

The best approximating model for roost-site selection by LFs incorporated distance to nearest mid-rotation stand and distance to nearest mixed pine-hardwood stand with a 35.4% probability (Table 3.3). This model was 1.5 times more likely than the next best approximating model, which contained the same parameters plus distance to nearest corridor. The confidence set of models included the top 6 models with a sum of Akaike weights of 0.85. Distance to nearest mixed pine-hardwood stand was negatively related and distance to nearest mid-rotation stand was positively related with site selection (Table 3.4). All other distance measures had model averaged 90% confidence intervals that included zero. Distance to nearest mixed pine-hardwood stand had the highest importance value, followed by distance to nearest mid-rotation stand. The composite model contained 2 variables whose scaled OR were relatively precise (Table 3.5). Lactating female evening bats were 17% more likely to select a site for every 25 m decrease in distance to nearest mixed pine-hardwood stand. Roost sites were 11% less likely to occur for every 25 m decrease in distance from nearest mid-rotation stand. Our top model for roost-site selection by LFs incorrectly predicted 18% of used sites as random and 23% of random sites as roosts. Based on our classification rates, our top model classified 75% of roosts and 83% of random sites correctly.

DISCUSSION

Evening bats in our study selected roosts in a variety of tree species, structure types, and habitat conditions. Miles et al. (2006) observed similar results for evening bats in southwest Georgia. As forest conditions frequently change on intensively managed landscapes, plasticity in roost selection likely allows bats to adjust to variations in forest structure and composition (Waldien et al. 2000, Miles et al. 2006). Similar to Boyles and Robbins (2006), we found

evening bats roosting primarily in tree cavities (77% M, 36% PF, 57% LF, 89% NF). Cavity roosts were located in mature pine, mixed pine-hardwood and hardwood stands. Mature forest stands provide numerous tall, large-diameter trees in later stages of decay suitable for cavity-roosting bats (Cryan et al. 2001). In mid-rotation and younger mature pine stands (range: 15–34 years), evening bats typically selected roosts in fork-topped pine trees. Fork-topped trees are frequently used by evening bats, particularly reproductive females, in southeastern managed pine forests and may provide an alternative to older trees (Menzel et al. 2001, Miles et al. 2006, D. A. Miller, Weyerhaeuser Company, unpublished data).

Tree-level characteristics of evening bat day-roosts varied between sex and among reproductive conditions. Compared to reproductive female bats, male and NF bats selected shorter, smaller structures as day-roosts. Small roosts, shaded by overstory trees may offer cooler conditions allowing male and NF bats to enter daily torpor and minimize energy expenditure (Hamilton and Barclay 1994). The use of tall, large-diameter trees by reproductive female bats is well documented (Kalcounis-Rüpell 2005). Reproductive female bats roost communally in large trees presumably to reduce thermoregulatory costs (Kurta 1986). Such roosts increase solar exposure and can spatially accommodate more individuals, thus increasing internal roost temperature which likely aid in prenatal growth and juvenile survival (Racey and Swift 1981, Lewis 1993). In addition, cavities in large-diameter trees possess thicker walls providing greater thermal stability and increased permanence (Kurta 1985).

Results of our model comparisons suggest the importance of mixed pine-hardwood stands for both male and LF evening bats. Mixed pine-hardwood stands, used by evening bats, consisted of late-successional habitat >50 years. In contrast, previous studies observed evening bats roosting primarily in pine (Menzel et al. 1999, 2001), hardwood (Boyles and Robbins 2006)

or both pine and hardwood stands (Miles et al. 2006). Menzel et al. (2001) located 93% of evening bats in longleaf pine (*P. palustris*) stands >45 years. Boyles and Robbins (2006) found evening bats roosting exclusively in mature hardwood habitat. Miles et al. (2006) tracked 78% of bats to mature longleaf pine stands (>70 years) on a natural longleaf pine landscape and 48% to riparian hardwood stands (>50 years) on an intensively managed pine landscape. Evening bats appear to select stands based on availability of mature forest across the landscape. Mature forests, regardless of habitat type, likely offer a greater variety of tree species and structure types used by cavity-roosting bats.

Distance to nearest corridor was negatively related to roost-site selection by male and LF evening bats suggesting the importance of forested corridors to these groups. Hein et al. (in press) reported similar findings for summer roosting Seminole bats. Because insect abundance can be greater along forested edges (Lewis 1970); close proximity of roosts to corridor stands may provide suitable commuting and foraging areas for bats. Landscape features, such as tree lines, hedgerows, and forested corridors also may function as navigational references and offer protection from wind and potential predators (Limpens and Kapteyn 1991, Verboom and Huitema 1997, Estrada and Coates-Estrada 2001, Murray and Kurta 2004).

Corridors also provide suitable roosting habitat for forest bats. We found nearly 20% of female and 40% of male evening bat roosts located within upland corridors comprised of pine or mixed pine-hardwood stands. Hein et al. (in press) also documented a high proportion of Seminole bat day-roosts in similar corridor stands. Contrary to Miles et al. (2006), we did not find evening bats roosting in riparian hardwood stands retained as streamside management zones (SMZs). On our site, SMZs were comprised of bottomland hardwood forests dominated by bald cypress and tupelo (*Nyssa* spp.). Tree species frequently used by evening bats on our site (i.e.,

loblolly pine, red maple) were not common in these stands. Furthermore, evening bats may select roosts in upland sites to reduce competition with two other cavity roosting species, Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) and southeastern myotis (*Myotis austroriparius*) closely associated with bottomland hardwood forests (Clark 2003).

Compared to random sites, male roosts were located farther from open stands. Previous landscape-level studies on forest bats have reported similar findings (Elmore et al. 2004, Miles et al. 2006). Although bats frequently forage over or near open habitat (Grindal and Brigham 1998, Jung et al. 1999, Patriquin and Barclay 2003, Elmore et al. 2005), selecting roosts offering optimal thermal conditions and protection may outweigh commuting costs (Racey and Swift 1981). In our study, male bats remained in diurnal roosts for multiple days, forgoing nightly foraging bouts suggesting the importance of roost selection over commuting distance. Lactating female bats roosted farther from mid-rotation pine stands compared to random sites. Mid-rotation stands likely do not provide suitable structures (i.e., tall, large-diameter trees) used as maternity colonies for lactating female bats and their pups. Furthermore, mid-rotation stands may not offer optimal foraging opportunities for bats due to high clutter (Erickson and West 1996).

Differences in selection criteria likely are influenced by distinct physiological demands between male and female bats during summer. Our findings were consistent with recent studies which demonstrated differential roost selection between sexes (Broders and Forbes 2004, Elmore et al. 2004, Hein et al., in press) and further emphasize the need for additional sex-specific studies. Although we were unable to model roost-site selection for pregnant or non-reproductive female evening bats, our data suggests differences exist among these reproductively distinct groups.

MANAGEMENT IMPLICATIONS

Our results concur with Miles et al. (2006) in that evening bats exhibit plasticity in roost selection allowing them to exploit changes in forest structure and composition. Although evening bats primarily roosted in mature stands, other forest conditions typically found on managed pine landscapes may provide additional roosting opportunities. Evidence of evening bats roosting in fork-topped pine trees in managed forests across the southeastern United States is well documented (Menzel et al. 2001, Miles et al. 2006, D. A. Miller, Weyerhaeuser Company, unpublished data). Retaining fork-topped trees through harvest rotations likely will increase potential roosting habitat for evening bats on managed pine forests. However, because evening bats typically select roost structures (i.e., snags and cavity trees) associated with late-successional forests, we recommend maintaining stands ≥ 50 years across managed landscapes to preserve vital roosting habitat. One means of retaining suitable roosting areas for bats is the creation and maintenance of forested corridors. Our study, along with Hein et al. (in press), demonstrated the use of forested corridors by both cavity- and foliage-roosting bats common to the southeastern United States. Additional research is needed to further elucidate the influence of forested corridors on the roosting and foraging habits of other bat species in the South.

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Table 3.1. Variables measured at summer roosts and random sites of evening bats (*Nycticeius humeralis*) in southern South Carolina, 2003-2006.

Scale	Variable	Definition
Tree	Tree Height (ht)	Height (m) of the tree
	Roost Height (rht)	Height (m) of the roost
	DBH (dbh)	Diameter (cm) at breast height of the roost tree
Plot	Basal area (ba)	Density (m ² /ha) of trees in a stand
	Overstory height (oht)	Average height (m) of overstory trees
Stand	Stand age (age)	Age (years) of stand
Landscape	Corridor (dcorr) ^a	Distance (m) to nearest corridor
	Edge (de) ^a	Distance (m) to nearest edge or road
	Open (do) ^a	Distance (m) to open stand
	Closed (dc) ^a	Distance (m) to closed stand
	Mid-rotation (dmr) ^a	Distance (m) to mid-rotation stand
	Mature pine (dmp) ^a	Distance (m) to mature pine stand
	Pine-hardwood (dph) ^a	Distance (m) to pine-hardwood stand
	Hardwood (dh) ^a	Distance (m) to hardwood stand

^aIncluded in global model

Table 3.2. Mean ($\pm$ SE) of 14 habitat variables measured at summer roosts and random sites of evening bats (*Nycticeius humeralis*) in southern South Carolina, 2003-2006. Variables are defined in Table 1.

Variable	Male ($n = 31$)				LF ($n = 24$)				PF ($n = 11$)				NF ($n = 9$)			
	Roost		Random		Roost		Random		Roost		Random		Roost		Random	
	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
ht	16.6	1.3	19.3	1.2	24.9	1.0	22.4	1.4	22.3	1.5	20.3	2.4	16.9	3.2	20.2	2.7
rht	8.6	0.7	8.1	0.6	10.2	0.9	7.8	0.7	8.9	0.7	7.4	0.7	8.7	1.5	8.0	1.4
dbh	22.3	2.4	28.8	2.1	36.6	2.9	31.2	2.2	32.4	2.7	31.7	3.7	23.0	4.6	32.5	3.7
ba	48.9	3.4	41.8	1.9	44.0	3.4	41.5	2.6	45.6	3.4	41.0	2.4	48.3	5.5	41.1	6.0
oht	20.4	0.5	20.0	0.5	20.7	0.5	21.2	0.5	20.5	0.6	20.0	0.5	22.1	0.9	19.8	0.8
age	46.9	3.7	13.6	2.8	48.1	3.7	12.6	2.3	37.4	6.9	25.2	8.7	50.9	5.4	22.3	7.9
dcorr ^a	255	43	477	58	319	72	481	61	459	97	520	185	261	78	243	86
de ^a	61	11	80	13	54	11	93	16	89	19	60	21	73	18	29	8
do ^a	283	46	165	44	114	21	131	39	285	82	404	131	205	58	153	50
dc ^a	556	108	474	90	896	157	667	106	352	151	474	134	162	33	554	179
dmr ^a	212	54	210	39	295	59	183	41	139	53	112	41	141	40	159	88
dmp ^a	448	69	420	70	301	51	495	87	670	102	608	129	509	124	723	210
dph ^a	182	37	422	66	125	41	483	74	259	77	399	138	157	68	429	127
dh ^a	1234	175	1303	167	1249	193	1218	166	1747	216	1312	258	2077	315	637	245

^aIncluded in global model

Table 3.3. Model selection results for the confidence set of models used to predict summer roost-site selection by evening bats (*Nycticeius humeralis*) in southern South Carolina, 2003–2006. Variables are defined in Table 1.

Model	K	AICc	Δ AICc	ω_i	R ²
Males					
dcorr do dph	4	71.3101	0.000	0.6851	0.4183
do dph	3	75.6626	4.352	0.0777	0.3149
Lactating females					
dmr dph	3	48.3178	0.000	0.35426	0.5375
dcorr dmr dph	4	49.1488	0.831	0.23382	0.5628
de dmr dph	4	50.5541	2.236	0.11580	0.5399
dmp dph	3	51.8000	3.482	0.06211	0.4776
dcorr dmp dph	4	52.5574	4.296	0.04253	0.5061
dcorr dph dh	4	52.6143	4.855	0.04134	0.5052

Table 3.4. Model-averaged estimates of summer roost-site selection by evening bats (*Nycticeius humeralis*) in southern South Carolina, 2003-2006. Variables are defined in Table 1.

Variable	Estimate	SE	L 90% CI	U 90% CI	Importance
Males					
intercept	1.1484	0.682	0.0299	2.267	1.00000
dph	-0.0033	0.001	-0.0054	-0.0012	0.94288
dcorr	-0.0028	0.001	-0.0048	-8.5E-04	0.87065
do	0.0034	0.002	9.3E-04	0.0059	0.84240
dc	4.0E-04	6.4E-04	-6.4E-04	0.0015	0.06545
dh	-2.2E-04	3.3E-04	-7.6E-04	3.1E-04	0.05982
dmp	3.4E-04	8.5E-04	-0.0011	0.0017	0.05207
dmr	-3.1E-05	0.001	-0.0020	0.0019	0.04890
de	-0.0028	0.005	-0.0109	0.0053	0.03895
Lactating females					
intercept	1.3221	1.041	-0.3855	3.0297	1.00000
dph	-0.0064	0.002	-0.0098	-0.0029	0.99961
dmr	0.0041	0.002	0.0011	0.0071	0.72438
dcorr	-0.0017	0.001	-0.0037	3.7E-04	0.38516
de	-0.0025	0.007	-0.1370	0.0086	0.17914
dmp	0.0019	0.002	-0.0043	6.2E-04	0.14923
dh	-5.2E-04	5.4E-04	-0.0014	3.7E-04	0.08339
do	0.0056	0.005	-0.0028	0.0139	0.07331
dc	2.0E-04	7.8E-04	-0.0011	0.0015	0.05130

Table 3.5. Odds ratios for estimates of summer roost-site selection by evening bats (*Nycticeius humeralis*) in southern South Carolina, 2003-2006. Variables are defined in Table 1.

Variable	OR	Unit Change	Scaled OR	Lower 90% CI Scaled OR	Upper 90% CI Scaled OR
Males					
dph	0.9967	25	0.9207	0.8738	0.9702
dcorr	0.9972	25	0.9322	0.8877	0.9789
do	1.0034	25	1.0892	1.0236	1.1590
dc	1.0004	25	1.0101	0.9840	1.0369
dh	0.9998	25	0.9992	0.9813	1.0079
dmp	1.0003	25	1.0084	0.9740	1.0440
dmr	0.9999	25	0.9992	0.9525	1.0482
de	0.9972	10	0.9726	0.8968	1.0548
Lactating females					
dph	0.9937	25	0.8529	0.7825	0.9297
dmr	1.0041	25	1.1081	1.0285	1.1940
dcorr	0.9983	25	0.9589	0.9112	1.0092
de	0.9975	10	0.9749	0.8720	1.0900
dmp	0.9982	25	0.9548	0.8977	1.0155
dh	0.9995	25	0.9871	0.9654	1.0093
do	1.0056	25	1.1490	0.9317	1.4171
dc	1.0002	25	1.0049	0.9734	1.0375

CHAPTER 4

SEX-SPECIFIC SUMMER ROOST-SITE SELECTION BY SEMINOLE BATS IN RESPONSE TO LANDSCAPE-LEVEL FOREST MANAGEMENT³

³ Hein, C. D., S. B. Castleberry, and K. V. Miller. Accepted by *The Journal of Mammalogy*. Reprinted here with the permission of the publisher.

ABSTRACT

Although importance of forested corridors to navigating and foraging bats has been documented, the relationship between corridors and roost-site selection has not been studied. From late May to mid-August 2003–2006, we used radiotelemetry to investigate roost-site selection by Seminole bats (*Lasiurus seminolus*) on an intensively managed landscape with forested corridors in southern, South Carolina. We tracked 27 (10 male, 17 female) adult Seminole bats to 90 (41 male, 49 female) diurnal roosts. We found 61% ($n = 25$) of male and 63% ($n = 31$) of female roosts in forested corridors, which comprised 11% of the landscape. We modeled roost-site selection with logistic regression and used Akaike's Information Criterion for small samples (AIC_c) and Akaike weights to select models relating roost-site selection to landscape-level features. Our results indicated several factors (i.e., distance to nearest corridor and distance to nearest mature pine stand) influenced roost-site selection and that differences existed between males and females, and among female reproductive condition. Our data suggests landscape-level features are more important than tree- and plot-level characteristics for roosting by Seminole bats on this managed forest. Corridors may represent a feasible approach to maintaining suitable roosting habitat for Seminole bats in managed forest landscapes.

KEY WORDS Bats, corridors, forest management, *Lasiurus seminolus*, pine, *Pinus*, radiotelemetry, roost-site selection, Seminole bat, South Carolina

INTRODUCTION

For many species of bats, trees serve as day and night roosts, summer maternity colonies, and winter hibernacula (Fenton 1997). If bats have specific roost-site requirements, alterations

in forest structure and composition may negatively impact bat populations (Erickson and West 1996; Grindal 1998). Therefore, it is essential to understand roosting requirements to assess, predict, and maintain important habitat features (Grindal and Brigham 1999).

Creation and maintenance of forested corridors has been suggested as a management approach to conserve native flora and fauna, provide wildlife habitat, reduce erosion, enhance aesthetics, and facilitate wildlife movement (Hobbs 1992). Juxtaposition of late-successional corridors within a mosaic of younger forests contributes to landscape heterogeneity and possibly ecosystem maintenance, both perceived to be critical components in sustainable resource management (Franklin and Forman 1987). For bats, linear landscape elements may provide sources of insect prey, navigational references, shelter from wind, and protection from predators (Grindal and Brigham 1999; Limpens and Krapteyn 1991; Verboom and Huitema 1997). Because corridors typically contain older trees and greater complexity in structure and composition than surrounding stands, bats may select these areas for roosting. However, no studies have explicitly examined the relationship between forested corridors and roost-site selection by bats.

Previous studies have provided insight into small-scale characteristics of the roosting ecology of bats in summer. Bats typically select larger, taller trees in areas with more open canopies for roosting when compared to random structures (Kalcounis-Rüppell et al. 2005; Menzel et al. 1998; Perry and Thill 2007; Vonhof and Barclay 1996). Although these studies provide useful information regarding tree and plot characteristics, bats may respond more to stand- and landscape-level attributes (Cryan et al. 2001; Elmore et al. 2004; Miles et al. 2006). Roost locations may depend on proximity of other potentially limiting landscape features, such as water resources and foraging areas (Waldien et al. 2000). Furthermore, tree-roosting bats

typically exhibit high fidelity to specific sites by roosting in different trees within a small area (Cryan et al. 2001; Elmore et al. 2004; Lunney et al. 1988), suggesting that landscape-level features might be more important influences on roosting area than specific roost structures (Miller et al. 2003).

The Seminole bat (*Lasiurus seminolus*) is a common foliage-roosting species found at low to intermediate elevations throughout the southeastern United States (Wilkins 1987), yet little is known regarding its summer roosting habits. During summer, Seminole bats have been observed roosting in the canopy of live trees (Menzel et al. 1998, 1999, 2000; Perry and Thill 2007). As with other tree-roosting species (Elmore et al. 2004; Grindal 1998; Vonhof and Barclay 1996), roost fidelity by Seminole bats is low and they frequently switch among roosts in close proximity (Menzel et al. 2000; Perry and Thill 2007). Tree height, diameter at breast height (DBH), structure height above the canopy, and overstory basal area are important factors implicated in roost selection (Menzel et al. 1998, 2000; Perry and Thill 2007). However, information regarding influence of landscape-level features on roost-site selection by Seminole bats is limited.

Although the area covered by industrial forests in the southeastern United States is expected to remain relatively constant for the next 20 years (National Commission on Science for Sustainable Forestry 2005), increased intensity of forest management in some locations may result in shorter harvest rotations, loss of late-successional forests, and declining species diversity in local vegetation communities (Allen et al. 1996). Several studies have evaluated the response of bats to various harvesting strategies in the region (Elmore et al. 2004; Menzel et al. 2002; Miles et al. 2006). However, information regarding methods for maintaining bat habitat in intensively managed landscapes is lacking (Wigley et al. 2007). Our goal was to examine large-

scale characteristics of day-roosts of Seminole bats on an intensively managed landscape with forested corridors. Our specific aim was to provide information allowing the integration of habitat features beneficial to bats with forest management objectives.

MATERIALS AND METHODS

Study Area

We conducted our study across a 41,365-ha area owned by MeadWestvaco Corporation in southeastern South Carolina. This area is located in the Lower Coastal Plain physiographic province and is characterized by flat topography (slopes <2%) and elevations ranging from 20–30 m above mean sea level. Summers are warm and humid with monthly temperatures and precipitation averaging 27°C and 186 mm, respectively (NOAA-National Climatic Data Center, <http://www.ncdc.noaa.gov>).

The area is intensively managed for the production of pine loblolly (*Pinus taeda*) wood and fiber and consists of even-aged stands in various successional stages. Plantation stands typically are clearcut at approximately 20–25 years of age. Silvicultural treatments include site preparation and planting of cleared stands, 1 or 2 commercial thinnings, and vegetation management via fire, mechanical and chemical treatments. At the time of our study, MeadWestvaco employed a unique forest management system, known as Ecosystem-Based Forestry, designed to increase heterogeneity of wildlife habitat (Constantine et al. 2005). This approach maintained a system of approximately 100–200 m wide corridors comprised of late-successional habitat creating a diverse forest structure and composition across the landscape. Three types of corridors were retained in harvested areas: water quality corridors located on poorly drained soils, visual corridors along public roads, and habitat diversity corridors located

in upland areas. Forested corridors composed of mature pine, mixed pine-hardwood, or hardwood habitat constituted 11% of the total study area.

Capture, Radiotelemetry, and Habitat Sampling

We captured Seminole bats from late May through mid-August 2003–2006 using 2–4 mist-nets set across 9 randomly selected ponds. Ponds were located in open habitat and were distributed throughout the study area. We recorded mass (g), forearm length (mm), sex, reproductive condition (Racey 1988), and relative age (Anthony 1988) of captured bats. We attached 0.43-g (Biotrack, Wareham, Dorset, United Kingdom) or 0.33-g (Blackburn Transmitters, Nacogdoches, Texas) radiotransmitters to the back of adult Seminole bats using Skin Bond adhesive (Pfizer, Largo, Florida). Transmitter load (mean = 2.9%, range = 2.0–4.3%) was <5% body mass (Aldridge and Brigham 1988). We held bats for 20 min to allow adhesive to set and then released them at the site of capture. Capture and handling procedures were approved by the University of Georgia Institutional Animal Care and Use Committee (IACUC # 2003-10029-ml) and followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

We located day-roosts using telemetry receivers (TRX 2000S, Wildlife Materials, Inc., Murphysboro, Illinois) and 3-element Yagi antennas. We tracked bats daily, when possible, beginning the day after capture until the radio transmitter failed or was recovered. We focused our tracking efforts on new bats or those with fewer identified roosts (Miles et al. 2006). Roost trees were verified, when possible, by visual identification using binoculars or by observing evening emergences. We recorded roost locations using Geoexplorer III or Geoexplorer XT (Trimble Navigation, Sunnyvale, California) Global Positioning System (GPS) units. We imported coordinates into a Geographic Information System for analysis.

To characterize tree- and plot-level features, we collected quantitative data for all roost trees and an equal number of random structures (Table 4.1). To avoid overlap between roost and random trees and to ensure random trees were within the same forested stand, random trees were located 50-100 m from roosts in a random direction. We considered any live pine tree with a $\text{DBH} \geq 10$ cm as a candidate random tree. We recorded species, DBH (cm), and tree height (m) for all roost and random trees. We established a 0.04-ha circular plot (radius = 11.35 m) centered on each roost and random tree and recorded species, DBH, and height of all overstory trees. We calculated basal area (m^2/ha) and mean overstory height from our plot-level data. All diameters and heights were measured using a DBH tape (Spencer Products Co., Seattle, Washington) and 400LH laser hypsometer (Opti-Logic Corp., Tullahoma, Tennessee), respectively. We estimated roosting home ranges (area encompassing all day-roosts), for bats with ≥ 3 roosts, by the Minimum Convex Polygon method using the Convex Hull Extension (Jennes 2004) in ArcView 3.2 (ESRI, Redlands, California).

To examine stand- and landscape-level selection, we defined 6 stand types: open, closed, mid-rotation, mature pine, mixed pine-hardwood, and hardwood. Open stands included clearcut and regenerating stands ≤ 5 years old, non-productive fields, and wildlife openings (i.e., food plots). Closed stands were dense, unthinned stands (6–11 years) with complete canopy closure. Mid-rotation stands were 12–22 years with almost complete canopy closure. Silvicultural prescriptions (i.e., burning, thinning) often occurred in these stands creating a more open canopy. Mature pine stands consisted of upland ($>75\%$ pine basal area) stands ≥ 23 years. Mixed pine-hardwood stands were mature stands (≥ 23 years) containing $>25\%$ and $<75\%$ pine basal area located on poorly developed soils. Hardwood stands ($<25\%$ pine basal area), typically were >50 years and associated with riparian zones or areas with poorly drained soils. Approximately 25%

of the study area consisted of open stands, 15% was closed, 33% was mid-rotation, 6% was mature pine, 10% was mixed pine-hardwood, and 8% was hardwood.

We determined the area of potentially available habitat based the ecology of Seminole bats (Arnett 2007; Taylor 1999). . We used ArcView 3.2 to create a circular landscape (males: radius = 3.0 km, area = 2,827 ha; females: radius = 3.5 km, area = 3,848 ha) around 9 capture ponds. Because water sources were limited or ephemeral, bats likely remained close to these ponds. This radius represented the maximum distance flown from capture pond to a roost by individuals of each gender. Area covered by all landscapes constituted 62% and 84% of the total study area for male and female bats, respectively. All stand types were available in each landscape in relative proportion to the total study area.

We selected random sites from a grid of 250 points within each circular landscape. The number of random sites we selected within each landscape equaled the number of roost trees located per capture pond. We updated GIS layers each year with stand and landscape data to control for changes in availability of stand types among years. We recorded stand age for all roost and random sites. We measured distance (m) from each roost and random site to nearest edge or road and to nearest corridor. We also measured distances (m) to nearest edge of each stand type. A value of zero was assigned to the stand type in which the roost or random site was found (Conner et al. 2003; Miller et al. 2000). If bats select specific habitat types as roost sites, on average, roost locations should be closer to those habitats than expected at random (Miller et al. 2000). Because we used maximum distance traveled from capture pond to roost to define our available landscape, we did not include distance to water in our analysis.

Analysis and Model Development

We used distance measures to model landscape-level roost-site selection. We conducted correlation analysis to ensure no pairs of variables were highly correlated (Spearman's $r > 0.7$). Prior to model analysis, we separated our data by gender and further divided females into separate reproductive conditions. We defined reproductive female bats (RF) as either pregnant or lactating and non-reproductive females (NF) as non-parous or post-lactating. We created a global logistic regression model, using 7 distance measures, to describe roost-site selection by Seminole bats. We tested our global model, using data from each gender and reproductive condition, for goodness-of-fit using the Hosmer-Lemeshow statistic (Hosmer and Lemeshow 2000). In addition to our global model, we selected 30 of a possible 127 candidate models based on our hypotheses relating roost-site selection to landscape variables. We used the same set of candidate models for both male and female bats. All variables appeared in an equal number of models creating a balanced model set.

Multiple observations from the same animal may not represent independent samples (Lacki and Baker 2003, Miller et al. 2003). Also, animal relocations clustered in space are likely to exhibit more similar attributes than are locations far apart (Moore and Swihart 2005). This phenomenon results in violation of independence assumptions with consequences that include artificially narrow confidence intervals for parameter estimation, inflated Type I error rates, and erroneous conclusions regarding importance of predictor variables (Erickson et al. 2001; Legendre 1993). Therefore, prior to model analysis, we examined the spatial and temporal autocorrelation of our data. We fit our global logistic regression model with structure type (roost versus random) as the binary response and conducted an analysis of variance of the residuals using the bat or year as our independent variable (Rieman et al. 2006). Our results indicated no significant spatial or temporal autocorrelation. Given that the data were

independent, we conducted our analysis, using the roost as the experimental unit, by employing traditional logistic regression techniques (Sokal and Rohlf 1995).

We used the log-likelihood for each model to calculate Akaike's Information Criterion for small sample sizes (AIC_c). We calculated Akaike model weights (ω_i) to evaluate and select the most parsimonious model and to predict variable importance (Burnham and Anderson 2002). We calculated relative importance for each parameter by summing Akaike weights across all models. A confidence set of models was established by including those models with Akaike weights within 10% of the highest value, which is comparable with the minimum cutoff point suggested by Royall (1997). We calculated Nagelkerke's R^2 for all models, to assess variation explained by each model contained within the confidence set (Nagelkerke 1991).

We used model averaging to incorporate model selection uncertainty directly into parameter estimates and standard errors using Akaike weights (Burnham and Anderson 2002). We based all inferences of parameter effects on this composite model. We calculated odds ratios (OR) from averaged parameter estimates. However, because larger or smaller unit changes may be more ecologically interpretable, we calculated scaled OR when appropriate (Hosmer and Lemeshow 2000). We evaluated ecological importance of each variable in the composite model by computing 90% confidence intervals for the scaled OR and interpreting magnitude of the values within these intervals (Gerard et al. 1998).

We used leave-one-out cross validation as a means of determining predictive power of our selected model (Neter et al. 1996). This method omits one observation from the data, fits the regression model with the remaining ($n-1$) observations, and estimates probability of presence using the fitted model, repeating for all observations. Accuracy of the logistic regression model is estimated by examining prediction and classification error rates. We used an estimated

probability of presence ≥ 0.5 as criterion for presence. All analyses were conducted using SAS version 8.0 (SAS Institute 2001). We report values as means $\pm$ SE unless stated otherwise.

RESULTS

We radiotracked 27 adult Seminole bats (10 M, 7 RF, 10 NF) to 90 individual day-roosts (41 M, 21 RF, 28 NF). Both male and female bats roosted exclusively in the canopy of live loblolly pine trees. Roost trees typically were taller and larger than random trees (Table 4.2). Mean number of roost trees located/bat was 4.1 ± 0.9 (range = 1–9) for male, 3.0 ± 0.8 (range = 1–6) for RF, and 2.8 ± 0.4 (range = 1–5) for NF bats. On average, males switched roosts every 1.2 ± 0.1 days compared to 2.2 ± 0.4 for RF and 1.3 ± 0.1 for NF bats. Twenty-eight roosts (14 M, 2 RF, 12 NF) were located in mid-rotation, 36 (16 M, 12 RF, 8 NF) in mature pine, and 26 (11 M, 7 RF, 8 NF) in mixed pine-hardwood stands. Bats typically roosted in the same stand for the duration of the transmitter. Mean roosting home range was 0.46 ± 0.10 ha (range = 0.11–0.95 ha, $n = 7$) for males, 5.85 ± 3.26 ha (range = 0.9–12.0, $n = 3$) for RF, and 0.22 ± 0.03 ha (range = 0.17–0.33, $n = 7$) for NF bats. Seventy percent of male roosts were within 1 km (1.2 ± 0.12 km, range = 0.4–2.9 km) from point of capture compared to 67% of RF roosts (1.5 ± 0.3 km, range = 0.4–3.5 km) and 61% of NF roosts (1.1 ± 0.2 km, range = 0.4–3.0 km). Sixty-one percent ($n = 25$) of male roosts, 76% ($n = 16$) of RF roosts, and 54% ($n = 15$) of NF roosts were located in corridor stands.

We found no spatial (males: $F = 1.31$, $d.f. = 9, 72$, $P = 0.25$; reproductive females: $F = 0.97$, $d.f. = 6, 35$, $P = 0.46$; non-reproductive females: $F = 0.38$, $d.f. = 9, 46$, $P = 0.94$) or temporal (males: $F = 1.65$, $d.f. = 2, 79$, $P = 0.20$; reproductive females: $F = 0.42$, $d.f. = 3, 38$, $P = 0.74$; non-reproductive females: $F = 0.11$, $d.f. = 2, 53$, $P = 0.8890$) autocorrelation. We found no correlation among distance variables for male, RF, and NF bats (Spearman rank tests). Our

global model incorporated distance to nearest corridor, distance to nearest edge or road, and distances to 5 of 6 stand types. Because Seminole bats did not roost in hardwood stands and distance to hardwood stands was >1 km, we excluded the distance to hardwood stands variable prior to model analysis. The global model provided an adequate fit to the data for male (Hosmer-Lemshow GOF statistic = 9.81, $d.f.$ = 8, P = 0.28), RF (Hosmer-Lemshow GOF statistic = 5.22, $d.f.$ = 8, P = 0.73) and NF (Hosmer-Lemshow GOF statistic = 5.37, $d.f.$ = 7, P = 0.61) bats, respectively.

Roost-site Selection by Males

The best approximating model for roost-site selection by males incorporated distance to nearest corridor and distance to nearest open stand with a 53.4% probability (Table 4.3). This model was 2.5 times more likely than the next best approximating model, which contained the same parameters plus distance to nearest closed stand. The confidence set of models included the top 4 models with a sum of Akaike weights of 0.895 indicating a 89.5% chance that 1 of these models was the best approximating model based on the data and set of candidate models. There was insufficient evidence to consider the remaining models as plausible explanations for roost-site selection. Distance to nearest corridor, distance to nearest edge, and distance to nearest open stand were negatively related to site selection (Table 4.4). Distances to nearest closed, mid-rotation, mature pine, and mixed pine-hardwood stands had model averaged 90% confidence intervals that included zero, indicating they provided little information about roost-site selection. Distance to nearest corridor had the highest importance values, followed by distance to nearest open stand and distance to nearest edge. The composite model contained 3 variables whose scaled OR were relatively precise (90% confidence interval does not include 1: Table 4.5). Roost sites were 20% and 21% less likely to occur for every 25 m increase in distance to nearest

corridor and distance to nearest open stand, respectively. The odds of a roost occurring decreased by 26% for every 10 m increase in distance from nearest edge. We evaluated model performance for male roost-site selection using the top model from our confidence set. The top model incorrectly predicted 18.0% of used sites as random and 20.9% of random sites as roosts. Based on our classification rates, our top model classified 78.1% of roosts and 82.9% of random sites correctly.

Roost-site Selection by Reproductive Females

The best approximating model for roost-site selection by RFs incorporated distance to nearest edge and distance to nearest mature pine stand with a 63.7% probability (Table 4.3). This model was 2.8 times more likely than the next best approximating model, which contained the same parameters plus distance to nearest mixed pine-hardwood stand. The confidence set of models included the top 2 models with a sum of Akaike weights of 0.862. Distance to nearest edge and distance to nearest mature pine stand were negatively related with site selection (Table 4.4). All other distance measures had model averaged 90% confidence intervals that included zero. Distance to nearest edge had the highest importance value, followed by distance to nearest mature pine stand. The composite model contained 2 variables whose scaled OR were relatively precise (Table 4.5). Reproductive female Seminole bats were 95% more likely to select a site for every 10 m decrease in distance to nearest edge. Roost sites were 18% less likely to occur for every 25 m increase in distance from nearest mature pine stand. Our top model for roost-site selection by RF Seminole bats incorrectly predicted 15.0% of used sites as random and 18.2% of random sites as roosts. Based on our classification rates, our top model classified 81.0% of roosts and 85.7% of random sites correctly.

Roost-site Selection by Non-reproductive Females

The best approximating model for roost-site selection by NFs incorporated distance to nearest corridor and distance to nearest edge with a 26.7% probability (Table 4.3). This model was 1.36 times more likely than the next best approximating model, which contained distance to nearest corridor and distance to nearest open stand. The confidence set of models included the top 10 models with a sum of Akaike weights of 0.93. Distance to nearest corridor was negatively related with site selection (Table 4.4). All other distance measures had model averaged 90% confidence intervals that included zero. Distance to nearest corridor had the highest importance value. The composite model contained 1 variable whose scaled OR was relatively precise (Table 4.5). Non-reproductive female Seminole bats were 9.2% more likely to select a site for every 25 m decrease in distance to nearest corridor. Our top model for roost-site selection by NF Seminole bats incorrectly predicted 30.4% of used sites as random and 36.4% of random sites as roosts. Based on our classification rates, our top model classified 57.0% of roosts and 75.0% of random sites correctly.

DISCUSSION

Our findings are consistent with previous radiotracking studies in that Seminole bats tended to roost in pine-dominated stands and select tall, large-diameter pine trees as day-roosts (Menzel et al. 1998, 1999, 2000; Perry and Thill 2007). Importance of tree height and DBH for foliage-roosting bats is well documented (Kalcounis-Rüppell et al. 2005). Larger trees may be easier to access and relocate, and offer greater protection from terrestrial predators (Mager and Nelson 2001; Vonhof and Barclay 1996). We found, on average, RF bats selected taller and larger trees compared to male or NF bats (Table 2). Reproductive female bats may benefit energetically from increased solar exposure, aiding growth of prenatal and juvenile bats (Racey and Swift 1981; Vonhof and Barclay 1996; Willis and Brigham 2005).

Previous radiotracking studies have emphasized importance of plot-level variables (i.e., overstory basal area) in roost selection (Menzel et al. 1998, 2000, Perry and Thill 2007). However, we found little difference between roost and random sites at this scale. Our study differs from previous ones in that random trees were located within the same stand as roost trees. Because managed forests generally contain even-aged stands with equally spaced trees of similar size, homogeneity within stands is likely greater than among stands. This may account for plot-level similarities between roost and random structures in our study. However, differences in plot-level features may exist in managed landscapes with greater within-stand heterogeneity.

We found that Seminole bats frequently switched roosts. Low roost fidelity is typical for foliage-roosting bats (Elmore et al. 2004; Menzel et al. 1998), but likely depends on species and geographic location (Willis and Brigham 2005). Lewis (1995) noted that bats occupying spatially abundant, less permanent roosts (i.e., trees) were more likely to change roosts frequently. Potential benefits of roost switching must outweigh time and energy costs associated with locating suitable roost sites. Bats that frequently switch roosts often remain faithful to particular areas apparently benefiting from site familiarity (Lewis 1995).

We found roosts of Seminole bats in close proximity to one another which resulted in small roosting home ranges for both genders. Menzel et al. (1998) also observed a small roosting home range for Seminole bats in South Carolina and Georgia. Similarly, red bats (*L. borealis*) exhibit high fidelity for clusters of trees (Elmore et al. 2004; Mager and Nelson 2001). The combination of low roost fidelity and high site fidelity suggests stand and landscape features may be more influential to roost-site selection compared to tree and plot characteristics (Cryan et al. 2001; Elmore et al. 2004; Lunney et al. 1988).

We found male and female bats roosting in older stands compared to random sites. With the exception of 2 bats (1 M, 1 NF), all roosts were located in stands ≥ 20 years old. Mature forest habitats have been reported to be important to roost selection (Hutchison and Lacki 2000; Menzel et al. 2000, 2002; Miles et al. 2006; Perry and Thill 2007). Tree-roosting bats tend to select late-successional stands because they contain large trees in areas with a more open canopy (Kalcounis-Rüppell et al. 2005). Although older stands appear important for site selection by both genders, our results do not indicate exclusive selection of mature forest stands by Seminole bats. This is evident by persistent use of roosts in mid-rotation stands. Over 34% of male and 43% of NF roosts occurred in these stands. The rapid growth rate of loblolly pine trees in intensively managed landscapes may produce taller, larger trees, suitable for use as roosts, at younger ages.

Results of our model comparisons suggest there are differences in habitat selection between sexes and reproductive condition. Similarly, Encarnação et al. (2005) observed sex-related differences in roost-site selection by Daubenton's bats (*Myotis daubentonii*). We found roosts of males relatively evenly distributed among mid-rotation, mature pine, and mixed pine-hardwood stands. In contrast, Perry and Thill (2007) found a majority of roosts of male *L. seminolus* in mixed pine-hardwood stands. Similar to adult red bats in Mississippi, we found males roosting near open stands (Elmore et al. 2004). Kunz (1982) suggested that habitat selection may be driven by the interaction between foraging and roosting requirements. Roosts located near open stands may reduce commuting flight distance to potential foraging areas (Grindal and Brigham 1999; Patriquin and Barclay 2003; Loeb and O'Keefe 2006). In contrast, RF bats were closely associated with mature pine habitat. These stands may offer more suitable roost sites for RF bats and developing young. Although females have high energy demands

during pregnancy and lactation, selecting roosts that offer optimal thermal conditions may outweigh commuting costs (Racey and Swift 1981; Kerth et al. 2001; Willis and Brigham 2005). Non-reproductive females did not select for any particular stand type. Non-parous and post-lactating bats may not require specific roosting conditions given the lack of reproductive demands.

Distance to nearest corridor was negatively related to roost-site selection by males and NFs, suggesting the importance of this stand type. Numerous studies have documented use of linear landscape features with respect to navigation, foraging, and protection (Grindal and Brigham 1999; Limpens and Krapteyn 1991; Verboom and Huitema 1997). Estrada and Coates-Estrada (2001) showed that bats of varying sizes, gender, age-class, and feeding guilds use live fence and stream corridors in southern Mexico for foraging. They concluded that corridors are important in reducing isolation distance between forest fragments by facilitating movement of bats in the landscape. Walsh and Harris (1996) demonstrated importance of corridors both for orientation and foraging in Britain. In our study, 61% of male, 76% of RF, and 54% of NF roosts were in corridor stands. Corridors consisting of mature pine and mixed pine-hardwood stands provided suitable roosting habitat for Seminole bats. Riparian hardwood corridors, typically retained in commercial forests as streamside management zones (SMZs), were not used by Seminole bats. Similar findings were reported by Perry and Thill (2007). In Mississippi, only adult male red bats roosted in SMZs (Elmore et al. 2004). In contrast, Miles et al. (2006), found a high proportion of roosts of evening bats (*Nycticeius humeralis*) in SMZs on the managed site, suggesting that using SMZs may depend on roosting strategy (foliage- versus cavity-roosting).

Our success rates in classifying roost and random sites for males and reproductive females implies we did not exclude any biologically significant variables from our models relating roost-site selection to landscape-level characteristics. Our results are consistent with previous studies that have demonstrated differential roost selection between genders (Broders and Forbes 2004; Elmore et al. 2004; Encarnação et al. 2005). Our classification rates for NF bats suggest either this group is not as selective as other gender/reproductive classes, or that we failed to measure important selection variables (Elmore et al. 2004). However, our data indicate that differences between RF and NF females exist. We did not distinguish among changes in reproductive condition of female bats. Because energy demands likely differ between pregnancy and lactation, changes in roost-site selection may exist. Additional research is needed to examine effects of pregnancy and lactation on roost-site selection by Seminole bats.

The summer roosting behavior of Seminole bats suggests that in managed landscapes they may respond more to large-scale features than to habitat variables measured at smaller spatial scales. Managing for larger scale features may represent a more effective and efficient approach compared to managing for site-specific characteristics. We recommend retaining areas, at least as large as the roosting home range, of suitable roosting habitat interspersed across the landscape. Furthermore, patches of suitable habitat should contain numerous potential roost trees in relatively close proximity (Perry and Thill 2007; Wigley et al. 2006).

Miller et al. (2003) recommended conducting research across an array of forest landscapes to examine impacts of various harvest strategies on bat populations. We examined roost-site selection within a uniquely managed landscape. Juxtaposition of late-successional corridors within a mosaic of younger, even-aged stands may represent an economically feasible and ecologically sound method for maintaining important bat habitat features in intensively

managed landscapes. We found that mature pine and mixed pine-hardwood corridors provided suitable roosting habitat for Seminole bats in our study. However, other factors may also be important for roost-site selection. Seminole bats appear to select clusters of tall, large-diameter pine trees near the edge of older, pine-dominated stands regardless of stand type. Use of forested corridors is a relatively new concept in intensively managed southern pine forests. Additional research is needed to demonstrate the effectiveness of corridors in providing suitable roosting and foraging habitat for other bat species.

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Table 4.1. Variables measured at summer roosts and random sites of Seminole bats (*Lasiurus seminolus*) in southern South Carolina, 2003-2006.

Scale	Variable	Definition
Tree	Height (ht)	Height (m) of tree
	DBH (dbh)	Diameter (cm) at breast height of tree
Plot	Basal area (ba)	Density (m ² /ha) of overstory trees in a stand
	Stems/ha (stems)	Number of trees in a stand (stems/ha)
	Overstory height (oht)	Average height (m) of overstory trees
	Percent pine (pine)	Percentage (%) of pine trees
Stand	Stand age (age)	Age (years) of stand
Landscape	Corridor (dcorr) ^a	Distance (m) to nearest corridor
	Edge (de) ^a	Distance (m) to nearest edge or road
	Open (do) ^a	Distance (m) to open stand
	Closed (dc) ^a	Distance (m) to closed stand
	Mid-rotation (dmr) ^a	Distance (m) to mid-rotation stand
	Mature pine (dmp) ^a	Distance (m) to mature pine stand
	Pine-hardwood (dph) ^a	Distance (m) to pine-hardwood stand
	Hardwood (dh)	Distance (m) to hardwood stand

^aIncluded in global landscape model.

Table 4.2. Mean and standard error of variables measured at summer roosts and random sites of Seminole bats (*Lasiurus seminolus*) in southern South Carolina, 2003-2006. Variables are defined in Table 1.

Variable ^a	Males (<i>n</i> = 41)				Reproductive females (<i>n</i> = 21)				Non-reproductive females (<i>n</i> = 28)			
	Roost		Random		Roost		Random		Roost		Random	
	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
ht	27.2	0.7	25.5	0.8	31.4	0.9	26.9	1.0	28.5	0.8	25.6	0.9
dbh	36.2	1.8	30.7	1.9	44.4	2.0	41.8	2.7	42.2	2.2	37.9	2.2
ba	32.3	1.7	34.5	2.0	36.0	3.1	28.9	2.1	36.1	1.9	38.4	2.4
stems	664.6	48.4	729.3	44.9	610.7	58.2	709.5	62.6	710.7	47.2	767.0	53.9
oht	21.0	0.4	20.6	0.4	20.2	0.8	18.1	0.6	20.1	0.8	19.7	0.5
pine	65.9	5.6	61.9	6.0	41.8	7.3	27.1	7.0	59.0	5.5	57.7	6.5
age	32.7	2.5	20.2	3.3	45.0	2.8	23.4	5.0	38.1	3.7	23.7	4.6
dcorr ^a	76.3	19.3	396.4	48.7	184.4	74.3	354.2	45.5	153.8	35.3	405.9	72.1
de ^a	33.5	4.9	112.2	14.4	21.5	2.9	85.7	17.3	58.5	10.3	55.7	8.9
do ^a	66.8	8.3	215.2	34.7	73.4	16.5	256.4	59.0	305.2	46.6	254.1	59.8
dc ^a	405.7	54.3	378.6	56.5	284.1	83.5	422.8	78.1	261.3	46.9	308.1	57.8
dmr ^a	342.3	67.9	200.9	34.7	313.3	74.7	157.4	44.8	120.6	24.6	139.7	30.3
dmp ^a	381.9	71.1	564.0	63.5	89.5	31.7	616.9	104.5	367.7	67.1	538.9	73.6
dph ^a	429.4	95.3	399.8	76.1	253.0	84.5	328.9	66.9	229.1	55.0	381.0	91.7
dh	1192.5	63.3	1022.9	127.9	1397.2	184.2	802.7	152.3	1363.1	142.1	1351.7	179.9

^aIncluded in global landscape model.

Table 4.3. Model selection results for the confidence set of models used to predict summer roost-site selection by Seminole bats (*Lasiurus seminolus*) in southern South Carolina, 2003-2006. Variables are defined in Table 1.

Model	K	AICc	$\Delta AICc$	ω_i	R^2
Males					
dcorr do	3	72.8440	0.00	0.5337	0.5830
dcorr do dc	4	74.6575	1.81	0.2155	0.5866
dcorr do dc dmr	5	76.7225	3.87	0.0767	0.5885
dcorr de	3	76.9350	4.09	0.0690	0.5446
Reproductive females					
de dmp	3	31.0484	0.00	0.6369	0.7372
de dmp dph	4	33.1315	2.08	0.2248	0.7424
Non-reproductive females					
dcorr de	3	71.5721	0.00	0.1987	0.2672
dcorr do	3	72.1905	0.62	0.1458	0.2553
dcorr dmr	3	72.5284	0.96	0.1232	0.2488
dcorr dmr dmp dph	5	72.5602	0.99	0.1212	0.3362
dcorr dph	3	73.3093	1.73	0.0833	0.2336
dcorr dmp	3	73.3721	1.80	0.0808	0.2323
dcorr dc	3	73.9236	2.35	0.6131	0.2214
dcorr dmp dph	4	74.4073	2.84	0.4814	0.2574
dcorr do dc	3	74.4839	2.91	0.4633	0.2559
dcorr do dc dmr	5	75.8001	4.23	0.0240	0.2768

Table 4.4. Model-averaged estimates of summer roost-site selection by Seminole bats (*Lasiurus seminolus*) in southern South Carolina, 2003-2006. Variables defined in Table 1.

Variable	Estimate	SE	L 90% CI	U 90% CI	Importance
Males					
intercept	2.2245	0.627	1.1951	3.2538	1.00000
dcorr	-0.0073	0.002	-0.0106	-0.0040	0.94774
do	-0.0075	0.003	-0.0130	-0.0021	0.90286
dc	0.0007	0.001	-0.0010	0.0024	0.35918
de	-0.0237	0.010	-0.0408	-0.0067	0.15292
dmr	-0.0005	0.001	-0.0022	0.0012	0.11795
dmp	1.4E-04	9.9E-04	-0.0015	0.0018	0.03989
dph	2.1E-04	6.0E-04	-0.0008	0.0012	0.03774
Reproductive females					
intercept	3.9433	1.476	-1.5228	6.3639	1.00000
dmp	-0.0067	0.003	-0.0112	-0.0022	0.99369
de	-0.0671	0.036	-0.1263	-0.0080	0.93070
dph	-9.9E-04	0.001	-0.0034	0.0014	0.32110
dmr	6.0E-06	0.002	-0.0035	0.0035	0.07389
dcorr	-0.0014	0.002	-0.0043	0.0015	0.02436
do	-0.0040	0.005	-0.0115	0.0035	0.01311
dc	-4.7E-04	0.001	-0.0026	0.0017	0.00960
Non-reproductive females					
intercept	1.1164	0.868	-0.2945	2.5273	1.00000
dcorr	-0.0035	0.001	-0.0059	-0.0012	0.94662
dmp	-0.0016	0.001	-0.0037	0.0005	0.30519
dmr	-0.0040	0.003	-0.0088	0.0008	0.30429
dph	-0.0011	9.6E-04	-0.0027	0.0005	0.29738
do	0.0014	0.001	-0.0006	0.0034	0.23637
de	0.0092	0.007	-0.0018	0.0203	0.23276
dc	-0.0004	0.001	-0.0023	0.0015	0.15067

Table 4.5. Odds ratios for estimates of summer roost-site selection by Seminole bats (*Lasiurus seminolus*) in southern South Carolina, 2003-2006. Variables are defined in Table 1.

Variable	OR	Unit Change	Scaled OR	L 90% CI Scaled OR	U 90% CI Scaled OR
Males					
dcorr	0.993	25	0.833	0.7671	0.9045
do	0.993	25	0.828	0.7227	0.9497
dc	1.001	25	1.019	0.9753	1.0623
de	0.977	10	0.789	0.6652	0.9352
dmr	0.999	25	0.988	0.9457	1.0317
dmp	1.000	25	1.003	0.9635	1.0450
dph	1.000	25	1.005	0.9809	1.0303
Reproductive females					
dmp	0.993	25	0.846	0.7550	0.9469
de	0.935	10	0.511	0.2830	0.9232
dph	0.999	25	0.976	0.9185	1.0363
dmr	1.000	25	1.000	0.9172	1.0906
dcorr	0.999	25	0.965	0.8987	1.0370
do	0.996	25	0.905	0.7508	1.0912
dc	0.999	25	0.988	0.9366	1.0428
Non-reproductive females					
dcorr	0.996	25	0.916	0.8633	0.9713
dmp	0.998	25	0.960	0.9114	1.0120
dmr	0.996	25	0.905	0.8031	1.0191
dph	0.999	25	0.973	0.9354	1.0124
do	1.001	25	1.036	0.9858	1.0885
de	1.009	10	1.097	0.9821	1.2247
dc	0.999	25	0.990	0.9451	1.0371

CHAPTER 5

SELECTION OF WINTER DAY-ROOSTS BY MALE SEMINOLE BATS ON AN
INTENSIVELY MANAGED SOUTHERN PINE FOREST⁴

⁴ Hein, C. D., S. B. Castleberry, and K. V. Miller. To be submitted to *The Journal of Wildlife Management*.

ABSTRACT

Understanding year-round roost-site selection is essential for managing forest bat populations. From January to March 2004–2006, we used radiotelemetry to investigate winter roost-site selection by Seminole (*Lasiurus seminolus*) bats on an intensively managed landscape with forested corridors in southern South Carolina, USA. We modeled roost-site selection with logistic regression and used Akaike's Information Criterion for small samples (AIC_c) and Akaike weights to select models relating roost-site selection to plot- and landscape-level variables. We tracked 20 adult male bats to 71 individual roosts. Bats used a variety of roosting structures, including the canopy of overstory trees, understory vegetation, pine needle clusters, and leaf litter. Roost height, structure type, and habitat type were influenced by changes in minimum nightly temperature. On warmer nights, bats selected taller trees in mature forest stands, but when minimum nightly temperatures were $<4^{\circ}\text{C}$, bats typically were found roosting on or near the forest floor in mid-rotation stands. Our results suggest that roosting strategies of Seminole bats differ between summer and winter seasons. Management decisions should incorporate year-round changes in roost-site selection to effectively manage forest bats.

KEY WORDS AIC, bats, *Lasiurus seminolus*, pine, *Pinus*, radiotelemetry, roost-site selection, Seminole bat, South Carolina, winter

INTRODUCTION

Understanding how seasonal changes affect roost-site selection is essential to effectively manage forest bat communities. Roosts are a fundamental aspect of bat ecology, providing sites for social interactions, protection from predators, and suitable thermoregulatory conditions

(Morrison 1980, Fenton 1983, Vaughan 1987). However, few studies have investigated seasonal changes in roost-site selection. Recently, Miller et al. (2003) and Kalcounis-Rüegg et al. (2005) synthesized over two decades of research concerning summer roost-site characteristics. Although the numerous studies cited in these reviews provide insight into summer roosting habits of bats, their level of inference is limited to one season.

Seasonal changes in roost-site selection have been reported for tree-roosting bats. Indiana bats (*Myotis sodalis*) select snags as summer roosts, but are found hibernating in caves and mines during winter (Kurta and Rice 2002). In summer, southeastern foliage-roosting species such as Seminole (*Lasiurus seminolus*) and red (*L. borealis*) bats typically roost in the canopy of overstory trees (Menzel et al. 1998, 2000, Hutchinson and Lacki 2000, Elmore 2004, Perry and Thill 2007, Hein et al., in press). However, these species appear to select alternate roosts in other seasons. Forest managers conducting winter burns have observed red bats flying from ground roosts in response to advancing prescribed fires (Saugey et al. 1989) and several authors have reported use of leaf litter by lasiurine bats (Saugey et al. 1998, Moorman et al. 1999, Rodrigue et al. 2001, Hein et al. 2005, Mormann and Robbins 2007). Leaf litter likely provides thermal benefits during extreme winter weather by reducing heat loss through convection and radiation (Whitaker and Stauffer 2003). Despite numerous reports of bats winter roosting on the ground, it is still unclear how frequently and under what conditions leaf litter roosts are used by roosting lasiurine bats.

In temperate regions, winter research can be problematic due to low levels of bat activity (Hayes 1997). Winter activity levels decrease as many bat species migrate to warmer latitudes or hibernate in caves, crevices, or human-made structures (Fleming and Eby 2003, Speakman and Thomas 2003). As a result, forest and wildlife managers have relied on summer data to create

year-round management strategies for forest bat populations. The paucity of information regarding winter roost-site selection suggests seasonal shifts in roosting behavior are not incorporated in existing management plans. Our objectives were to examine winter roost-site selection by Seminole bats, compare our results on winter roosting habits with previous summer studies, and provide guidelines for timing management prescriptions to minimize potential negative impacts on winter roosting bats.

STUDY AREA

We conducted our study on MeadWestvaco Corporation's South Region in southern South Carolina, USA. The study area is located in the Lower Coastal Plain physiographic province and is characterized by flat topography (slopes <2%) and elevations ranging from 20–30 m above mean sea level. Winters are cool and dry with monthly temperatures and precipitation averaging 12.6° C and 8.81 cm respectively (NOAA-National Climatic Data Center, <http://www.ncdc.noaa.gov>).

The 41,365 ha area is intensively managed for loblolly pine (*Pinus taeda*) wood and fiber products and consists of even-aged stands in various successional stages. Plantation stands typically are clearcut at approximately 20–25 years of age. Silviculture includes site preparation and planting of cleared stands, 1 or 2 commercial thinnings, and vegetation management via fire, mechanical and chemical treatments. At the time of our study, MeadWestvaco employed a unique forest management system, known as Ecosystem-Based Forestry, designed to increase heterogeneity of wildlife habitat across the landscape (Constantine et al. 2005). This approach maintained a system of approximately 100–200 m wide forested corridors within a mosaic of even-aged stands creating a diversity of forest structure and composition across the landscape.

These forested corridors, composed of mature pine, mixed pine-hardwood, or hardwood stands, constituted 11% of the total study area.

METHODS

From January to March 2004–2006 we captured Seminole bats using 2–4 mist-nets 6 m to 12 m in length set over 8 randomly selected ponds. Ponds were located in open areas, adjacent to roads, and distributed throughout the study area. For each captured bat, we recorded mass (g), and forearm length (mm), sex, and relative age (Anthony 1988). We attached 0.43-g (Biotrack, Wareham, Dorset, UK) or 0.33-g (Blackburn Transmitters, Nacogdoches, Texas, USA) radiotransmitters to the back of adult Seminole bats using Skin Bond surgical adhesive (Pfizer, Largo, Florida, USA). Transmitter load (mean = 3.5%, range = 2.9%–4.4%) was <5% body mass (Aldridge and Brigham 1988). We conducted bat capture and handling under University of Georgia Institutional Animal Care and Use Committee guidelines (IACUC # 2003-10029-ml).

We located day-roosts using telemetry receivers (TRX 2000S, Wildlife Materials, Inc., Murphysboro, Illinois, USA) and 3-element Yagi antennas. We tracked bats daily, when possible, beginning the day after capture until the transmitter failed or was recovered. We focused our tracking efforts on new bats or those with fewer identified roosts (Miles et al. 2006). Roosts were verified, when possible, by visual identification. We recorded roost locations using a Geoexplorer III or Geoexplorer XT (Trimble Navigation, Sunnyvale, California, USA) Global Positioning System (GPS) unit. We imported coordinates into a Geographic Information System (GIS) for analysis. We randomly placed 3 HOBO data loggers (Onset Computer Corp., Bourne, Massachusetts, USA) set 1.5 m above the ground in open habitat to continuously record ambient

temperatures throughout the study. Because roost selection occurs at night, we used minimum nightly temperature for our analyses.

Habitat Sampling

To assess tree- and plot-level characteristics, we collected quantitative data for all roosts and an equal number of random structures (Table 5.1). We selected random structures matching those used by bats. To avoid overlap between roost and random structures and to ensure random sites were in the same forested stand, random structures were located 50-100 m from roosts in a random direction. We recorded species, diameter at breast height (DBH: 1.4 m from base of tree), structure height and roost height for all non-leaf litter roost and random structures. We established a 0.04-ha (radius = 11.35 m) circular plot centered on each roost and random structure and recorded species, DBH, and height of all overstory trees (DBH ≥ 10 cm) in the plot. We calculated basal area (m^2/ha) and mean overstory height from our plot-level data. We measured all diameters and heights using a DBH tape (Spencer Products Co., Seattle, WA) and 400LH laser hypsometer (Opti-Logic Corp., Tullahoma, TN), respectively. We estimated roosting home range (area encompassing all day-roosts), for bats with ≥ 3 roosts (Mormann and Robbins 2007), by the Minimum Convex Polygon method using the Convex Hull Extension (Jennes 2004) in ArcView 3.2 (ESRI, Redlands, California, USA).

To examine stand- and landscape-level features, we first divided our study area into 6 stand types: open, closed, mid-rotation, mature pine, mixed pine-hardwood, and hardwood. Open stands included clearcut and regenerating stands ≤ 5 years old, non-productive fields, and wildlife openings (i.e., food plots). Closed stands were dense, unthinned stands (6–11 years) with complete canopy closure. Mid-rotation stands were 12–22 years old with almost complete canopy closure. Silvicultural prescriptions (i.e., burning, thinning) often occurred in these stands

creating a more open canopy. Mature pine stands consisted of upland pine ($>75\%$ pine basal area) stands ≥ 23 years. Mixed pine-hardwood stands were mature stands (≥ 23 years) containing 25% – 75% pine basal area located on poorly developed soils. Hardwood stands ($<25\%$ pine basal area) typically were >50 years old and associated with riparian zones or areas of poorly drained soils. Approximately 25% of the study area consisted of open habitat, 15% was closed, 33% was mid-rotation, 6% was mature pine, 10% was pine-hardwood, and 8% was hardwood.

We determined the area of potentially available habitat based on observed Seminole bat ecology (Taylor 1999, Arnett 2007). We created circular landscapes (radius = 2.7 km, area = $2,290$ ha) around 8 capture ponds using ArcView 3.2. This radius represented the maximum distance flown from capture pond to roost by an individual bat. Because water sources were limited or ephemeral, bats likely remained close to these ponds. All stand types were available in each landscape in relative proportion to the total study area

We selected random sites from a grid of 250 points within each circular landscape. The number of random sites we selected in each landscape equaled the number of roost structures located per capture pond. We updated GIS layers each year with stand and landscape data to control for changes in availability of stand types among years. We recorded stand age for all roost and random sites located per capture pond. We measured distance (m) from each roost and random site to nearest edge or road and to nearest corridor. We also measured distances (m) to nearest edge of each stand type. A value of zero was assigned to the stand type in which the roost or random site was found (Miller et al. 2000, Conner et al. 2003). If bats select specific habitat types as roost sites, on average, roost locations should be closer to those habitats than expected at random (Miller et al. 2000). Because we used the maximum distance traveled from

capture pond to roost to define our available landscape, we did not include distance to water in our analysis.

Analysis and Model Development

We conducted correlation analysis to ensure no pairs of variables were highly correlated (Spearman's $r > 0.7$). We fit a global logistic regression model using structure type (roost vs. random) as the binary response and 8 plot- and landscape-level explanatory variables. Tree-level variables did not apply to all structures and therefore were not included in model analysis. We tested our global model for goodness-of-fit using the Hosmer-Lemeshow statistic (Hosmer and Lemeshow 2000). We conducted an analysis of variance of the residuals from our global model, using the bat or year as our independent variable, to examine spatial and temporal autocorrelation of our data (Rieman et al. 2006). Our results indicated no spatial or temporal autocorrelation. Because our data were independent, we conducted our analysis, with the roost as the experimental unit, by employing traditional logistic regression (Sokal and Rohlf 1995). We divided our dataset into two groups, warm- (WR) and cold-weather (CR) roosts, based on the minimum nightly temperature the roost was selected ($WR \geq 4^\circ \text{C}$; $CR < 4^\circ \text{C}$) and analyzed each group separately. We based our cutoff on changes in roost selection (i.e., roost height, structure type, and stand type) we observed above or below this temperature. In addition to our global model, we selected 67 of a possible 511 candidate models based on our hypotheses relating roost-site selection to plot and landscape variables. All variables appeared in an equal number of models creating a balance model set.

We used the log-likelihood for each model to calculate Akaike's Information Criterion for small sample sizes (AIC_c). We calculated Akaike model weights (ω_i) to evaluate and select the most parsimonious model and predict variable importance (Burnham and Anderson 2002).

We created a confidence set of models by including models with Akaike weights within 10% of the highest value, which is comparable with the minimum cutoff point suggested by Royall (1997). We calculated Nagelkerke's R^2 for all models to assess variation explained by each model contained in the confidence set (Nagelkerke 1991).

We used model averaging to incorporate model selection uncertainty directly into parameter estimates and standard errors using Akaike weights (Burnham and Anderson 2002). We calculated odds ratios (OR) from averaged parameter estimates. However, because larger or smaller unit changes may be more ecologically interpretable, we calculated scaled OR when appropriate (Hosmer and Lemeshow 2002). We evaluated the ecological importance of each variable in the composite model by computing 90% confidence intervals for scaled OR and interpreting the magnitude of values in these intervals (Gerard et al. 1998).

We used leave-one-out cross validation as a means of determining the predictive power of our selected model (Neter et al. 1996). We used an estimated probability of presence ≥ 0.5 as the criterion for presence. We compared roost aspects with a random circular distribution using Rayleigh's test (Zar 1999). All analyses were conducted using SAS version 8.0 (SAS Institute, 2001). We report values as means $\pm$ SE unless stated otherwise.

RESULTS

We radiotracked 20 male Seminole bats to 71 (38 WR, 33 CR) individual roosts. No female bats were captured during our study. Eighty-one percent of roosts were within 1.5 km (0.86 ± 0.07 km, range = 0.13–2.65 km) from point of capture. On average, bats used 4.2 ± 0.39 roosts (range = 1–7 roosts). We observed individual bats roosting in the same structure for up to 12 days. Individuals selected a different day-roost across a variety of nightly temperatures (range = -7.78 – 16.11° C), however, 60% of roost-switching occurred on nights with

temperatures $>4^{\circ}\text{C}$, and 93% on nights with temperatures $>0^{\circ}\text{C}$. Mean roosting home range was 10.0 ± 4.3 ha (range = 0.07–58.78 ha, $n = 16$ bats). Size of roosting home range was not correlated with the number of day roosts located ($r = 0.206$, $P = 0.45$). On one occasion, four bats were observed roosting in the same stand (area = 68.7 ha) with two roosts located 6.5 m from each other.

Roost structures included the canopy of overstory hardwood trees (15 WR, 9 CR), canopy of overstory loblolly pine trees (10 WR, 4 CR), understory canopy (4 WR, 1 CR), pine needle clusters suspended from understory vegetation (9 WR, 10 CR), and pine leaf litter (0 WR, 9 CR). Seminole bat roosts were located in mid-rotation (14 WR, 16 CR), mature pine (10 WR, 11 CR), and mixed pine-hardwood (14 WR, 6 CR) stands. Five bats (5 WR, 4 CR) were found roosting in forested corridor stands. Mean stand age was 34.0 ± 2.75 years (range = 16–64 years) and 29.1 ± 2.53 years (range = 14–61 years) for WR and CR, respectively (Table 5.2). Mean roosting aspect for both WR (aspect = 173.7° , $z = 9.34$, $P < 0.001$, $n = 31$) and CR (aspect = 174.5° , $z = 4.08$, $P < 0.001$, $n = 19$) differed significantly from a random circular distribution.

Roost-site selection varied with minimum nightly temperature. On warm nights ($>4.0^{\circ}\text{C}$), bats typically roosted in the canopy of overstory trees. On cooler nights ($<4^{\circ}\text{C}$) bats tended to roost lower in the canopy (≤ 5.0 m) or select alternative roosts (i.e., pine needle clusters or leaf litter). Mean minimum nightly temperature was $2.36 \pm 0.64^{\circ}\text{C}$ and $-2.55 \pm 0.52^{\circ}\text{C}$ for pine needle cluster and leaf litter roosts, respectively. Temperature changes had little effect on stand type selected. However, on warmer nights, bats generally selected mixed pine-hardwood stands.

Our results indicated no significant spatial ($F_{19,51} = 0.42$, $P = 0.9849$) or temporal ($F_{2,68} = 1.79$, $P = 0.1704$) autocorrelation. Spearman tests showed no correlation among distance variables for winter roosting male bats. Our global model incorporated basal area, average

height of overstory trees, distance to nearest corridor, distance to nearest edge or road, and distance to 5 of 6 habitat types. Because Seminole bats did not roost in hardwood stands and distance to hardwood stands was >1 km, we excluded distance to hardwood habitat prior to model analysis. The global model provided an adequate fit to the data for WR (Hosmer-Lemeshow GOF statistic₈ = 7.7589, $P = 0.4574$), and CR (Hosmer-Lemeshow GOF statistic₇ = 6.5418, $P = 0.4781$).

Warm Weather Roost-site Selection

The best approximating model for WR selection contained basal area, and distances to nearest mid-rotation and mixed pine-hardwood stands with a 41.5% probability (Table 5.3). This model was 3 times more likely than the next best approximating model, which contained the same predictors, but also included distance to nearest corridor. The confidence set of models included the top 4 models. The sum of Akaike weights for the confidence set was 0.782 indicating a 78.2% chance that 1 of these models was the best approximating model based on the data and set of candidate models. There was insufficient evidence to consider the remaining models as plausible explanations for WR selection. Basal area, distance to nearest mid-rotation and distance to nearest mixed pine-hardwood stands were negatively related with site selection (Table 5.4). Three variables (distance to nearest corridor, distance to nearest edge, and distance to nearest mature pine stand) included within the confidence set had model-averaged 90% confidence intervals that included zero, indicating they provided little information regarding roost-site selection. Basal area had the highest importance value, followed closely by distance to nearest mixed pine-hardwood stand. Distance to nearest mid-rotation stand also had a high importance value. The composite model contained three variables whose scaled OR were relatively precise (90% confidence interval does not include 1: Table 5.5). Odds of a bat

roosting in a stand increased by 33.0% for every 5 m²/ha decrease in basal area. Roost sites were 8.0% and 5.0% less likely to occur for every 25 m increase in distance to nearest mixed pine-hardwood and nearest mid-rotation stands, respectively. We evaluated model performance for warm roost-site selection using the top model from our confidence set. The top model incorrectly predicted 34.3% of used sites as random and 36.6% of random sites as roosts. Based on our classification rates, our top model classified 60.5% of roosts and 68.4% of random sites correctly.

Cold Weather Roost-site Selection

The best approximating model for CR selection contained basal area, distance to nearest edge, and distances to nearest mid-rotation and mature pine stands with a 27.0% probability (Table 5.3). This model was 1.9 times more likely than the next best approximating model, which contained basal area, distance to nearest edge, and distances to nearest mature pine and mixed pine-hardwood stands. The confidence set of models included the top 7 models. The sum of Akaike weights for the confidence set was 0.757. Basal area and distances to nearest mid-rotation and mature pine stands were negatively related, and distance to nearest edge was positively related with site selection (Table 5.4). Four variables (distance to nearest corridor, and distances to nearest closed, mid-rotation, and mixed pine-hardwood stands) included within the confidence set had model-averaged 90% confidence intervals that included zero. Basal area had the highest importance value, followed by distance to nearest mature pine stand and distance to nearest edge. The composite model contained three variables whose scaled OR were relatively precise (Table 5.5). Odds of a bat roosting in a stand increased by 36.8% for every 5 m²/ha decrease in basal area. Roost sites were 4.0% less likely to occur for every 25 m increase in distance to mature pine habitat. The top model for CR selection incorrectly predicted 29.7% of

used sites as random and 24.1% of random sites as roosts. Based on our classification rates, our top model classified 78.8% of roosts and 66.7% of random sites correctly.

DISCUSSION

Seminole bats frequently switched roosts in winter during warmer weather. This behavior is consistent with roost switching patterns observed by this species in summer (Menzel et al. 1998, 2000, Hein et al., in press). During colder weather, bats switched roosts less often, presumably remaining in the same location until more favorable conditions for relocating, foraging, or drinking (Brigham 1987, Speakman and Racey 1989, Thomas and Geiser 1997). Saugey et al. (1998) and Mormann and Robbins (2007) reported similar findings for red bats in Arkansas and Missouri, respectively. Bats also appeared to exhibit greater fidelity to individual winter roost structures rather than specific areas, as observed in summer (Hein et al., in press). We often found bats (64%, $n = 14$) returning to previously used trees or pine needle clusters. Bats likely save time and energy using roosts with known microclimate characteristics (Lewis 1995).

Winter roosting home ranges of male Seminole bats typically were larger compared to summer home ranges and included several different stand types of various ages. Mormann and Robbins (2007) also reported larger winter roosting home ranges for male red bats. In contrast, Menzel et al. (1998) found summer Seminole bat roosts in close proximity to one another with a mean roosting home range of 0.2 ± 0.1 ha. Similarly, Hein et al. (in press) reported male Seminole bats roosting in a small area (0.46 ± 0.1 ha) with all roosts typically in the same forested stand. Bats presumably require a greater suite of resources during winter in response to temperature fluctuations. Stands of various age classes and stand types likely offer different

microclimate conditions (Reagan 1974, Matlack 1993). Bats may select sites in winter based on ambient conditions to meet specific thermoregulatory demands.

We generally found Seminole bats roosting on the southeast side of trees. Similar results were reported for female hoary bat (*L. cinereus*) summer roosts in Saskatchewan, Canada (Willis and Brigham 2005). In contrast, Mager and Nelson (2001) reported the majority of red bat summer roosts on northern or eastern aspects, shaded from direct solar radiation. Increased solar exposure may be more important for bats in winter or colder climates (i.e., Canada). A southeastern roost aspect may optimize sun exposure and radiant heating for roosting bats, especially during cool morning hours (Willis and Brigham 2005).

Winter roost selection was more diverse compared to summer. Seminole bats roost almost exclusively in the canopy of live loblolly trees during summer (Menzel et al. 1998, Menzel et al. 2000, Perry and Thill 2007, Hein et al., in press). In contrast, winter roosts varied in height and structure type. At warmer temperatures, roost selection closely resembled that of summer bats with 66% of roosts located within the canopy of overstory trees. However, at colder temperatures bats selected roosts that offered additional shelter. We found 61% of cold roosts close to or on the forest floor. Bats typically selected roosts under leaf litter at temperatures $<0^{\circ}\text{C}$ and within pine-needle clusters suspended $\leq 5\text{ m}$ above the forest floor at temperatures $<4^{\circ}\text{C}$. The selection of alternate roosts may optimize thermoregulatory conditions essential for winter survival. Leaf litter and pine-needle clusters may reduce heat loss by bats and provide protection from adverse weather (Whitaker and Stauffer 2003).

Plot-level variables had a greater influence on roost-site selection in winter compared to summer. Basal area was an important predictor for both WR and CR selection. Winter roosting bats selected sites with less basal area compared to random sites (Table 2). In contrast, summer

roosts were located in stands with greater overstory basal area (Menzel et al. 1998, Hein et al., in press). Because winter roosts were located closer to the forest floor, less basal area likely reduced the amount of clutter and increased maneuverability within forested stands (Brigham et al. 1997). Moreover, less basal area surrounding roosts likely increased solar exposure, potentially aiding thermoregulation (Willis and Brigham 2005). Although we found no difference in average overstory height between roost and random sites, winter roost-sites were surrounded by a shorter canopy compared to summer sites. In Missouri, Boyles and Robbins (2006) observed similar results for winter roosting evening bats (*Nycticeius humeralis*). A shorter canopy height may benefit winter roosting bats by offering additional shelter from wind. Wind speeds tend to grade from high levels in open matrix habitat to low levels in the forest interior due to vegetation (Matlack 1993, Wilder et al. 2005).

Distance to nearest mid-rotation stand was negatively related to roost-site selection regardless of ambient temperature. Forty-two percent of all winter roosts were located in mid-rotation stands. In summer, male Seminole bats also selected mid-rotation habitat, however, most roosts were found in stands ≥ 20 years (Hein et al., in press). Only 3% of summer roosts were found in stands < 20 years compared to 39% of winter roosts. Younger stands typically have a lower canopy height and more complete canopy closure, possibly offering greater protection during periods of strong winds and cold temperatures (Matlack 1993, Davies-Colley et al. 2000).

Although model results showed similarities in habitat selection between warm- and cold-weather roosts, differences did exist. Bats typically selected pine-dominated stands during colder ambient temperatures. Loblolly pines provided 72% of all cold roosts. Although bats seldom roosted in the canopy of pine trees, the needles from overstory pines provided additional

roosts in the form of needle clusters and leaf litter. Because pine trees retain their leaves throughout the year, these stands may preserve heat and likely result in a more stable environment (Geiger 1966). Bats selected mixed pine-hardwood stands during the warmest temperatures. The absence of leaves on hardwood trees in winter likely increases the amount of solar radiation received by bats. Such roosts allow for passive re-warming of body temperatures, thus minimizing energy expenditure during arousal (Vaughan and O'Shea 1976, Neubaum et al. 2006).

We found bats roosting farther from edge during colder temperatures compared to random structures. However, no difference in distance to edge was observed for warm-weather roosts. Male bats were observed roosting farther from edge habitat (79.7 ± 10.6 m) in winter compared to summer (33.5 ± 4.9 m, Hein et al., in press). Because bats often roost on or near the ground and often have long arousal times (Thomas et al. 1990), they likely are more vulnerable to predation in winter. Roosting farther from edge may offer greater protection from predators (Hutchinson and Lacki 2000). Furthermore, roosts within the interior of stands likely are buffered from strong winds and cold temperatures (Davies-Colley et al. 2000). The potential security and shelter of interior forested stands, may have reduced the use of corridors by winter roosting bats (13%, roosts = 9) compared to summer (61%, roosts = 25, Hein et al., in press).

Roost-site selection apparently was related to ambient temperature. On warmer nights (temperature $\geq 4^\circ$ C), bats exhibited roosting behavior similar to that observed in summer (i.e., switching roosts daily) (Menzel et al. 1998, 2000, Hein et al., in press). Roosts were associated with older stands located in the canopy of overstory trees. As temperatures decreased, bats typically selected alternative roosts that provided additional shelter and remained in these roosts for ≥ 2 days. Often these roosts were in younger stands and were located on or near the forest

floor. However, given that our classification rates were <70%, these behaviors were not ubiquitous. On several occasions, bats using warm roosts failed to relocate on days when temperatures dropped suddenly before sunset. Bats undergoing daily torpor may be unable to arouse mid-day to select a more suitable roost (Thomas et al. 1990). Alternately, not all cold-weather roosts were on or near the ground as some bats selected large clumps of Spanish moss located high in the canopy (height >10 m) rather than roosting on or near the forest floor. Previous studies have documented Seminole bats using Spanish moss in winter (Constantine 1958, Jennings 1958). Spanish moss may provide similar insulatory properties as leaf-litter, thus protecting bats from cold temperatures (Menzel et al. 1999).

MANAGEMENT IMPLICATIONS

Our results indicate that roost-, plot-, stand-, and landscape-level selection by Seminole bats in winter differs from summer. Winter roost-site selection appears related to ambient temperatures presumably to optimize thermoregulatory conditions. We found bats selecting roosts offering additional shelter during cold periods and more exposed roosts at warmer temperatures. Therefore, forest and wildlife managers must supply a range of forest conditions to provide suitable habitat for bats throughout the year.

We found over 61% of winter roosts on or near the forest floor at temperatures <4° C. Because hibernating bats may take 30 to 60 minutes to arouse and reach activity levels sufficient to escape fires (Thomas et al. 1990), prescribed burns may result in direct mortality. Disturbance during periods of hibernation also may cause bats to lose energy reserves or become dehydrated (Speakman and Racey 1989). Furthermore, winter fires remove existing and potential roosting habitat by eliminating leaf litter and low hanging pine needle clusters. We recommend caution

when implementing prescribed burns on days when the previous night's temperature, as measured in open habitat, $<4^{\circ}\text{C}$ to minimize potential adverse impacts on winter roosting bats.

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Table 5.1. Variables measured at winter roosts and random sites of Seminole bats (*Lasiurus seminolus*) in southern South Carolina, 2004-2006.

Scale	Variable	Definition
Tree	Structure height	Height (m) of the structure
	Roost height	Height (m) of the roost
	DBH	Diameter (cm) at breast height of the tree
	Roost aspect	Aspect (°) of the roosting bat
Plot	Basal area (ba) ^a	Density (m ² /ha) of overstory trees in a stand
	Stems/ha (stems)	Number of trees in a stand (trees/ha)
	Overstory height (oht) ^a	Average height (m) of overstory trees
	Percent Pine (pine)	Percentage (%) of pine trees
Stand	Stand age (age)	Age (years) of the stand
Landscape	Corridor (dcorr) ^a	Distance (m) to nearest corridor
	Edge (de) ^a	Distance (m) to nearest edge or road
	Open (do) ^a	Distance (m) to open stand
	Closed (dc) ^a	Distance (m) to closed stand
	Mid-rotation (dmr) ^a	Distance (m) to mid-rotation stand
	Mature pine (dmp) ^a	Distance (m) to mature pine stand
	Pine-hardwood (dph) ^a	Distance (m) to pine-hardwood stand
	Hardwood (dh)	Distance (m) to hardwood stand

^aIncluded in global model

Table 5.2. Mean and standard error of variables measured at warm- and cold-weather winter roosts and random sites of Seminole bats (*Lasiurus seminolus*) in southern South Carolina, 2004-2006. Variables are defined in Table 1.

Variable	Warm Weather Sites ($\geq 4^{\circ}\text{C}$; $n=38$)				Cold Weather Sites ($<4^{\circ}\text{C}$; $n=33$)			
	Roost		Random		Roost		Random	
	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
ba	26.3	2.6	37.7	1.9	25.7	3.3	40.9	2.6
stems	784.2	61.4	871.9	53.7	903.0	66.6	999.2	68.7
oh ^a	17.5	0.5	18.0	0.4	17.8	0.4	18.1	0.3
pine	46.6	6.2	50.0	6.4	63.0	6.4	67.2	6.3
age	34.0	2.8	18.2	3.0	29.1	2.5	23.4	3.7
dcorr ^a	433.8	64.8	428.7	55.8	318.1	40.9	375.8	56.9
de ^a	75.3	15.3	122.0	14.2	84.8	14.7	57.0	8.6
do ^a	312.2	34.1	320.7	56.0	297.9	40.9	219.3	39.9
dc ^a	379.9	35.9	440.5	82.1	425.6	61.8	410.0	64.5
dmr ^a	120.8	38.2	238.5	39.4	152.0	43.2	261.4	41.0
dmp ^a	437.3	78.6	450.1	70.7	305.6	70.4	566.9	89.6
dph ^a	199.9	33.6	407.5	54.6	275.5	36.4	268.2	58.2
dh	1078.3	100.5	1346.3	153.9	1322.5	17.7	1357.7	162.7

^aIncluded in global model

Table 5.3. Model selection results for the confidence set of models used to predict winter roost-site selection by Seminole bats (*Lasiurus seminolus*) in southern South Carolina, 2004-2006. Variables are defined in Table 1.

Model ^a	K	AICc	Δ AICc	ω_i	R ²
Warm Roosts					
ba dmr dph	4	90.5614	0.00	0.41501	0.3532
ba dcorr dmr dph	5	92.7888	2.23	0.13627	0.3537
ba de dmr dph	5	92.8516	2.29	0.09859	0.3529
ba dmp dph	4	93.4361	2.87	0.03460	0.3150
Cold Roosts					
ba de dmr dmp	5	77.715	0.00	0.27044	0.4174
ba de dmp dph	5	79.103	1.30	0.14133	0.3992
ba dmr dmp	4	79.155	1.44	0.13165	0.3633
ba dcorr dmr dmp	5	79.933	2.22	0.08923	0.3861
ba de	3	80.993	3.28	0.05252	0.3010
ba dcorr do	4	81.430	3.72	0.04219	0.3293
ba de dc	4	82.113	4.40	0.03000	0.3189

Table 5.4. Model-averaged estimates of winter roost-site selection by Seminole bats (*Lasiurus seminolus*) in southern South Carolina, 2004-2006. Variables are defined in Table 1.

Variable	Estimate	SE	L 90% CI	U 90% CI	Importance
Warm Roosts					
intercept	2.9146	0.989	1.2925	4.5367	1.00000
ba	-0.0572	0.022	-0.0925	-0.0218	0.92792
dph	-0.0029	0.001	0.0048	-0.0010	0.91757
dmr	-0.0021	0.001	-0.0039	-2.5E-04	0.77387
de	-0.0008	0.003	-0.0069	0.0053	0.21531
dmp	-0.0006	6.4E-04	-0.0017	4.4E-04	0.20709
dcorr	-8.3E-05	8.8E-04	-0.0015	0.0013	0.19886
oht	-0.0660	0.071	-0.1818	0.0497	0.03131
do	0.0002	0.002	-0.0015	0.0019	0.02035
dc	-0.0003	0.001	-0.0014	8.6E-04	0.02005
Cold Roosts					
intercept	2.5917	1.164	0.6821	4.5012	1.00000
ba	-0.0625	0.023	-0.1000	-0.0249	0.97758
dmp	-0.0017	7.3E-04	-0.0023	-4.9E-04	0.70994
de	0.0087	0.005	0.0010	0.0164	0.56512
dmr	-0.0020	0.001	-0.0043	2.5E-04	0.54174
dcorr	-0.0017	0.001	-0.0037	3.2E-04	0.22518
dph	-5.6E-04	0.001	-0.0026	0.0015	0.21562
do	0.0018	0.001	-4.1E-04	0.0040	0.15484
dc	-9.8E-04	0.001	-0.0025	5.2E-04	0.11649
oht	0.0304	0.151	-0.2177	0.2785	0.02635

Table 5.5. Odds ratios for estimates of winter roost-site selection by Seminole bats (*Lasiurus seminolus*) in southern South Carolina, 2004-2006. Variables are defined in Table 1.

Variable	OR	Unit Change	Scaled OR	L 90%CI Scaled OR	U 90% CI Scaled OR
Warm Roosts					
ba	0.9445	5	0.7515	0.6297	0.8968
dph	0.9971	25	0.9297	0.8862	0.9754
dmr	0.9979	25	0.9491	0.9064	0.9937
de	0.9992	10	0.9925	0.9338	1.0550
dmp	0.9994	25	0.9849	0.9595	1.0111
dcorr	0.9999	25	0.9979	0.9624	1.0348
oht	0.9361	1	0.9361	0.8338	1.0510
do	1.0002	25	1.0060	0.9641	1.0498
dc	0.9997	25	0.9937	0.9664	1.0218
Cold Roosts					
ba	0.9394	5	0.7317	0.6064	0.8828
dmp	0.9983	25	0.9588	0.9304	0.9879
de	1.0088	10	1.0911	1.0102	1.1784
dmr	0.9980	25	0.9509	0.8988	1.0062
dcorr	0.9983	25	0.9592	0.9127	1.0081
dph	0.9994	25	0.9862	0.9363	1.0388
do	1.0018	25	1.0453	0.9899	1.1038
dc	0.9990	25	0.9759	0.9402	1.0130
oht	1.0309	1	1.0309	0.8044	1.3211

CHAPTER 6

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Silvicultural practices on intensively managed forest landscapes typically are not conducive to maintaining snags and older trees used by forest-dwelling bats (Miles et al. 2006). Forest product companies in the southeastern United States often manage using even-aged systems with short harvest rotations to meet rising demands for forest products (Wigley et al. 2007). However, bat conservation and intensive forest management are not mutually exclusive (Hayes 2003). Forest companies seeking to maximize economic, ecological, and social benefits generally manage for biological diversity under sustainable forestry guidelines (Wigley et al. 2007). Through their Ecosystem Based Forestry approach, the MeadWestvaco Corporation established a system of forested corridors on its South Region to maintain diversity of forest habitat across the landscape. My study was designed to investigate the influence of these corridors on forest-dwelling bats.

BAT ACTIVITY AND FORESTED CORRIDORS

I found high rates of bat activity associated with forested corridors. Bats were more active along corridor edge compared to interior corridor or adjacent stands. Results of my analyses indicate similarities in selection criteria among 6 species of forest bats. As predicted, bat use had a strong, positive relationship with edge for all species. In general, bats selected corridors with taller overstory trees and younger adjacent stands. The combination of these

features likely increases effective height and visibility of edge. Taller edge height also may provide greater abundance of insects and shelter from wind (Lewis 1970).

Based on echomorphology (Aldridge and Rautenbach 1987), I correctly predicted greater use of interior corridor stands by small-bodied, more maneuverable bats (i.e., *Myotis lucifugus*). Contrary to predictions, *Eptesicus fuscus* also showed a positive relationship with interior corridor stands. Although the echomorphology of this species (i.e., high wing-loading, low frequency calls) suggests it is better adapted for less cluttered habitats, it is possible that detections of *E. fuscus* originated from individuals flying above the forest canopy. Bats, particularly larger species, may use horizontal edge created by the ecotone between the forest canopy and open habitat above (Grindal and Brigham 1999, Kalcounis et al. 1999, Menzel et al. 2005).

My findings are consistent with previous studies documenting the use of linear landscape features (i.e., vegetation and stream corridors, tree lines, and hedgerows) by commuting and foraging bats (Limpens and Kapteyn 1991, Walsh and Harris 1996, Verboom and Huitema 1997, Verboom and Spoelstra 1999). Edge appears to be an important landscape component because it represents orderly and predictable clutter to commuting and foraging bats (Kalko and Schnitzler 1993). In addition, insect abundance and availability is often higher along forest edge (Lewis, 1970). Because corridors increase the amount of edge habitat across the landscape, they likely provide suitable commuting lanes and foraging habitat for forest bats.

SUMMER ROOST-SITE SELECTION

Evening bats selected roosts in a variety of tree species, structure types, and habitat conditions. Male bats roosted alone, primarily in tree cavities (77%), whereas females typically roosted colonially in tree cavities (56%) or fork-topped pine trees (34%). Cavity roosts primarily

were located in mature mixed pine-hardwood stands. In mid-rotation and younger mature pine stands (range: 15–34 years), evening bats typically selected roosts in fork-topped pine trees. Evidence of evening bats, especially reproductive females, roosting in fork-topped pine trees in managed forests across the southeastern United States is well documented (Menzel et al. 2001, Miles et al. 2006, D. A. Miller, Weyerhaeuser Company, unpublished data). Retaining fork-topped trees through harvest rotations may increase potential roosting habitat for evening bats on managed pine forests. However, because evening bats typically select roost structures (i.e., snags and cavity trees) associated with late-successional forests, I recommend maintaining stands ≥ 50 years across managed landscapes to preserve vital roosting habitat.

Seminole bats roosted exclusively in the canopy of tall, large-diameter pine trees. Roosts typically were located near edge in older (≥ 20 years), pine-dominated stands. Contrary to previous studies (Menzel et al. 1998, 2000, Perry and Thill 2007), I found little influence of plot-level variables on roost-site selection. Seminole bats exhibited low roost fidelity and high site fidelity suggesting stand and landscape features are more influential in roost-site selection compared to small-scale characteristics (Lunney et al. 1988, Cryan et al. 2001, Elmore et al. 2004). Thus, managing for large-scale features rather than site-specific characteristics may represent a more effective and efficient approach to providing suitable bat roosting habitat. Furthermore, patches of suitable habitat should contain numerous potential roost trees in relatively close proximity (Perry and Thill 2007; Wigley et al. 2007).

My results indicate sex-specific roost selection criteria for both species. In summer, female bats exhibit distinct physiological demands imposed during pregnancy and lactation. Reproductive female evening and Seminole bats selected taller, larger roosts located in interior forest stands presumably to increase protection and reduce thermoregulatory costs (Racey and

Swift 1981). My findings were consistent with recent studies that demonstrated differential roost selection between sexes (Broders and Forbes 2004, Elmore et al. 2004) and further emphasize the need for additional sex-specific studies.

My study demonstrated the use of forested corridors by both cavity- and foliage-roosting bats common to the southeastern United States. I found nearly 20% of female and 40% of male evening bat roosts, and over 60% of both male and female Seminole bat roosts located within upland corridors comprised of mature pine or mixed pine-hardwood stands. Riparian hardwood corridors, typically retained in commercial forests as streamside management zones (SMZs), were not used by either species. However, several studies have documented the importance of SMZ's in providing suitable roosting and foraging habitat for bats (Menzel et al. 2002, Menzel et al. 2005, Miles et al. 2006). On my site, SMZs were comprised of bottomland hardwood forests dominated by bald cypress and tupelo (*Nyssa* spp.). Tree species (i.e., loblolly pine, red maple) frequently used by evening and Seminole bats on my site were not common in these stands. Additional research is needed to further elucidate the influence of forested corridors on the roosting ecology of other bat species in the South.

WINTER ROOST-SITE SELECTION

My results indicate roost-, plot-, stand-, and landscape-level selection by Seminole bats differ between seasons. Variations in winter roost-site selection were related to ambient temperature. On warmer nights (temperature $\geq 4^{\circ}\text{C}$), bats exhibited roosting behavior similar to that observed in summer (Menzel et al. 1998, 2000, Perry and Thill 2007). As temperatures decreased, bats typically selected alternative roosts that provided additional shelter and remained in these roosts for ≥ 2 days. Cold-weather roosts often were in mid-rotation stands (12–22 years old) and located on or near the forest floor. Because bats required a greater suite of resources in

response to temperature fluctuations, forest and wildlife managers must supply a range of forest conditions to provide suitable habitat for winter-roosting bats.

Prescribed fires are a common mid-rotation silvicultural practice in forestry and wildlife habitat management. Winter burns conducted in southeastern managed forests may negatively impact winter roosting bats (Carter et al. 2002). I found over 61% of winter roosts on or near the forest floor at temperatures $<4^{\circ}\text{C}$. Because hibernating bats may take 30 to 60 minutes to arouse and reach activity levels sufficient to escape fires (Thomas et al. 1990), prescribed burns may result in direct mortality. Disturbance during periods of hibernation also may cause bats to lose energy reserves or become dehydrated (Speakman and Racey 1989). Furthermore, winter fires remove potential roosting habitat by eliminating leaf litter and low hanging pine needle clusters. I recommend caution when implementing prescribed burns on days when the previous night's temperature $<4^{\circ}\text{C}$ to minimize potential adverse impacts on winter roosting bats.

CONCLUSIONS

My study demonstrated the utility of forested corridors in providing suitable habitat for southeastern bats on an intensively managed pine landscape. Use of linear landscape features likely varies among species, region, habitat type, and level of prey abundance and availability. Regardless of use, linear elements appear to be an important landscape feature for many bat species around the world. I recognize that corridors cannot offset the overall loss of forest habitat. However, my results affirm that management practices designed to create and enhance corridors may represent an effective and ecologically sound method for maintaining important bat habitat features (i.e., edge and mature forest stands) and should be considered in management plans. Additional research is needed to demonstrate the response by bats to corridors in different regions and landscape conditions.

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