STAND- AND LANDSCAPE-LEVEL ROOST SELECTION BY FOREST BATS IN THE OUACHITA MOUNTAINS

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CHAPTER 1

SELECTION OF ROOSTING HABITAT BY FOREST BATS IN A DIVERSE FORESTED LANDSCAPE

Abstract. Forest management alters forest structure and composition, which affects quality and quantity of habitats available for roosting bats. Most studies of roost selection by forest-dwelling bats concentrated on microhabitat without providing forest stand-level preferences by bats; thus, those studies have provided limited information for managers. I evaluated diurnal summer roost selection by 6 species of bat at the forest-stand level in the Ouachita Mountains of west-central Arkansas. Over a 6-year period, I evaluated 428 roost locations for 162 individuals of 6 species. Using individual bats as the experimental unit, all 6 species were selective in their choice of roosting habitat. Bats generally preferred to roost in stands that contained mature (≥50 years old) trees but relatively few midstory trees. The most preferred habitat was mature, mixed pine-hardwood forest that had undergone recent partial harvest and midstory removal (thinned mature); 5 of 6 bat species roosted closer to that habitat ($P < 0.10$) than random locations, and 41.3% of roosts were located in that habitat class. Those habitats were composed of recently harvested single-tree selection and areas being restored to open pine woodlands. Although 24.6% of eastern pipistrelle (*Pipistrellus subflavus*) roosts were located in partially harvested stand, 90% of those roosts were located in unharvested buffer strips along ephemeral streams within those treated stands. The second most preferred habitat was old-growth (≥100 years old) mixed pine-hardwood forest; 4 of 6 bat species preferred that habitat class but it composed an average of only 3.5% of available habitat.

Although highly available, mixed pine-hardwood and hardwood second-growth forests 50−99 years of age were preferred by only by red bats (*Lasiurus borealis*); however, 19.9% of roosts from all species were located in that habitat class. Mature forest stands that have undergone thinning, midstory removal, and retention of large overstory pines, hardwoods, and snags provide quality roosting habitat for forest bats and may mimic historic open-forest conditions that were once prevalent throughout the eastern and southeastern U.S.

INTRODUCTION

Because roost sites of bats play an important role in thermoregulation and protection from predators, roost-site characteristics undoubtedly influence bat fitness and survival (Vonhof and Barclay 1996). In forested environments, bats roost primarily in trees and snags, but preservation of individual trees is usually not a viable management option (Fenton 1997). Rather, the goal of forest management should be to ensure that adequate roosting habitat is available spatially and temporally (Brigham et al. 1997a, Crampton and Barclay 1998, Rabe et al. 1998).

Tree-roosting bats of the Ouachita Mountain region can be divided into 2 groups based on their diurnal roosting habits: those that roost primarily in vegetation (leaves or needles) of tree canopies and those that roost in cavities and crevices of live trees and snags. Cavity and crevice-roosting bats roost in cracks, spaces under peeling bark, holes in decaying limbs, old woodpecker holes, and hollow trunks of live trees and snags (Christy and West 1993). The big brown bat (*Eptesicus fuscus*), evening bat (*Nycticeius humeralis*), and the northern longear myotis (*Myotis septentrionalis*) are cavity- and

crevice-roosting species. Four species of vegetation-roosting bats, which typically roost by hanging from leaf petioles or small branches and appear from the ground as dead leaves or pine cones (Constantine 1966, Menzel et al. 1998), occur in the Ouachita Mountains during summer: eastern red bats (*Lasiurus borealis*), Seminole bats (*L. seminolus*), eastern pipistrelles (*Pipistrellus subflavus*), and hoary bats (*L. cinereus*). Thus, benefits of senescent trees likely are of less importance for vegetation-roosting species than for cavity-crevice roosting species.

Many tree-roosting bats prefer large-diameter trees and snags for roosting (Tidemann and Flavel 1987, Barclay et al. 1988, Taylor and Savva 1988, Brigham 1991, Kalcounis 1995, Vonhof 1995, Brigham et al. 1997a, Crampton and Barclay 1998). Old-growth forests provide abundant old trees and large snags that are used by some bat species for roosting (Christy and West 1993). However, in the southeastern U.S., a diverse bat fauna exists although little old-growth forest exists and intensive forest management is common throughout much of the region (Bat Conservation International 2001, Conner and Hartsell 2002, Trani 2002). Although bats may prefer older trees because of their structural characteristics, many species may prefer less-cluttered (Mackey and Barclay 1989, Brigham et al. 1997b) or "open" habitats because of difficulties associated with flying in forests with dense and complex structure (Mackey and Barclay 1989, Burford and Lacki 1995, Menzel et al. 2002b). Further, increased solar radiation on roost trees located in more open stands may speed fetal and juvenile growth during reproduction (Racey and Swift 1981, Menzel et al. 2000, Vonhof 1996). In a meta-analysis of 56 published papers on roost selection by forest bats, Kalcounis-Ruppell et al. (2005) found that roost trees generally occurred in areas with lower canopy

cover than random locations, suggesting many bat species prefer to roost in relatively open forests. Thus, thinning forests to lower tree density, reducing midstory, burning to reduce woody understory vegetation, and retaining large overstory trees and snags may improve bat roosting and foraging habitat. These management practices are becoming increasingly more common on public lands in the southeastern U.S. as forest managers strive to restore ecosystems and reduce fuel hazards (e.g., Bukenhofer and Hedrick 1997, McMahon et al. 1998). However, the effects of these practices on bat roosting are largely unknown. Furthermore, many studies of bat roosting conducted in forested environments had a limited diversity of forest types and stand ages. True measurements of preference among habitats are limited if a wide array of habitats are not available to the species under study.

Analysis of stand-level roost selection is rarely conducted in studies of bats. Instead, studies typically compare habitat attributes such as canopy height and tree density surrounding roost sites with attributes of random points to isolate habitat characteristics that may influence roost selection (e.g., Sasse 1995, Hutchinson and Lacki 2000, Menzel et al. 2001). These habitat components are then extrapolated to the stand level. However, knowing how bats respond to specific silvicultural treatments, stand ages, and forest types is useful information for managers.

Roost selection by tree-roosting bats presents a complicated situation for stand-level selection analysis. Unlike studies examining animal movements within their home range that yield large numbers of locations, the number of roosts obtained for each bat is typically low due to limited life of radiotransmitters (about 2 weeks) and the ecology of roost selection. An individual bat may roost in a different location each day, whereas

another individual may select a single roost for the life of the transmitter. For example, red bats and Seminole bats switch roosts frequently (Menzel et al. 1998), whereas big brown bats, in areas with limited snag availability, rarely switch roosts during the period of radiotracking (Brigham 1991). Consequently, the majority of studies comparing stand-level availability with use for roosting utilized the method of Neu et al. (1974), which uses locations, not individual animals, as the experimental unit. Various authors have pointed out biases associated with using individual locations as the experimental unit in resource-selection studies (Johnson 1980, Aebischer et al. 1993, Miller et al. 2003). The Neu et al. (1974) method also does not allow for changes in habitat over time, nor does it allow habitat availability to be defined separately for each individual.

Categorical methods that use resource-selection functions (Manley et al. 1993) and multivariate analysis of variance (MANOVA), including compositional analysis (Aebischer et al. 1993) and the method of Arthur et al. (1996), use individuals as the experimental unit, define habitat availability for each individual separately, and can be used where habitat changes over time. However, these methods rely on the assumption of multivariate normality, which is not met with sparse data sets containing numerous zeros like those found in most roost studies. Distance measurements such as Euclidean distance statistics (DA; Conner and Plowman 2001) offer a way to use individuals as the experimental unit, define habitat availability for each individual separately, and do not result in data sets dominated by zeros, even when the number of observations per animal is low. Therefore, I used Euclidean distance measurements to evaluate selection of diurnal summer roosting habitat by 6 species of forest bats in a diverse forested landscape. I developed the following predictions regarding how bats may respond to

different habitats: 1) bats prefer to roost in stands that contain mature, relatively large pines and hardwoods (Kalcounis 1995, Vonhof 1995); 2) bats prefer roosting in relatively open stands with little midstory clutter (Sasse 1995, Campbell et al. 1996, Hutchinson and Lacki 2000); and 3) bats roost in proximity to open areas where foraging opportunities are abundant (Mackey and Barclay 1989, Burford and Lacki 1995, Grindal and Brigham 1998, Menzel et al. 2002b).

METHODS

Study area

The study was conducted in the 6,545-ha Upper Lake Winona Basin, situated in the Ouachita Mountains of west-central Arkansas (approx. 34°48'N, 92°58'W; Fig. 1.1). The Ouachita Mountains are a series of east-west oriented ridges and valleys that extend from central Arkansas into east-central Oklahoma. Elevations range from 152 to 853 m above mean sea level, mean annual precipitation ranges from 112 to 137 cm, and mean annual temperature ranges from 13.9 to 16.1 °C (Skiles 1981). The climate is semihumid to humid, with hot summers and mild winters.

No residential areas, farms, houses, agricultural lands, or pastures existed within the study portion of the basin. Although most of the basin consisted of mixed shortleaf pine (*Pinus echinata*)–hardwood forests managed by the U.S. Forest Service (USFS; Ouachita National Forest), the basin also contained a mix of other forest types, primarily oak (*Quercus* spp.)–hickory (*Carya* spp.). Twelve percent (778 ha) of the area was intensively managed industrial timberlands (owned by Weyerhaeuser Company, Tacoma, Washington, USA) consisting mostly of closed-canopy and older-thinned plantations of

loblolly pine (*Pinus taeda*) managed under a 30- to 35-year rotation. Those plantations generally were thinned and pruned at 15−20 years of age. Industrial timberlands contained abundant unharvested buffer strips (streamside management zones; SMZs), approximately 30−100 m wide, established around streams for water-quality protection; those SMZs were typically mature hardwood and mixed pine-hardwood forest

National forest lands within the basin were divided into six 513–1,791-ha management units where different silvicultural treatments were implemented in 2000 as part of the Ouachita Mountains Ecosystem Management Research and Demonstration Initiative (Guldin 2004). A 1,232-ha pine woodland restoration unit was thinned initially and burned with the long-term goal of obtaining an open woodland condition with an abundant herbaceous understory, maintained by periodic (3−5 years) prescribed burns. That area was thinned to 13.8 m^2/ha overstory basal area (BA); 1.1 m^2/ha of the total overstory BA was retained as overstory hardwoods. An 864-ha single-tree selection unit also was also thinned to 13.8 m^2/ha of overstory BA, with 2.3 m^2/ha of that being retained hardwoods. Both of the previous 2 treatments underwent partial midstory removal whereby nearly all hardwoods <15 cm dbh were felled. A 531-ha small group selection unit (openings of 0.4–0.81 ha) and a 513-ha large group selection unit (openings of 2.02–4.05 ha) consisted of patch cuts (essentially small clearcuts) where about 2.3 m^2/ha of overstory BA (primarily pine) was retained and all other trees were removed or felled. Pines in the forest matrix surrounding those openings were thinned to about 16.0 m^2/ha of overstory BA, but no hardwoods were removed. A 1,791-ha unit was managed using a mix of treatments and silvicultural systems, including group selection, single-tree

selection, and seed-tree cuts in stands of 16−18 ha. Seed-tree cuts had about 2.3 m^2/ha of retained pine overstory; all other trees were removed or felled.

On USFS lands, most harvested stands contained ephemeral stream drainages. Unharvested 15−50-m wide buffer strips (greenbelts henceforth) were established for water-quality protection around each drain. Those strips were primarily mixed pine-hardwood stands containing mature (≥50 years old) trees, and no cutting or midstory removal was conducted in greenbelts. Although exact proportions of stands that were retained greenbelt was unavailable, field observations suggested about 20% of most partially harvested stands (pine woodland restoration areas, single-tree selection, and group selection stands, collectively) were greenbelt. In addition, USFS lands contained SMZs along permanent and intermittent streams that were larger but similar in composition to greenbelts.

The basin also contained an 836-ha, largely untreated block, consisting mostly of mature second-growth pine-hardwood timber. Throughout the basin, stands that were either inoperable (e.g., too steep), in various stages of regeneration, uneconomical to harvest, or dominated by uneconomical forest types such as hardwoods were interspersed within treatments. Thus, with its north- and south-facing slopes, treatment units, untreated areas, and the industrial timberlands, the Winona Basin contained most of the predominant forest types and forest-management practices that existed in the Ouachita Mountains.

Bat capture and radiotelemetry

From mid-May until early August 2000−2005, I captured bats between 2100 and 0130 h CST at 21 trapping areas distributed throughout the basin. I trapped bats for 125 nights using 3−8 mist nets (2.6−12.0 m wide x 2.6 m high). Trapping locations were primarily stream pools but also included forest roads, ponds, bridges, road culverts, and dry creek beds. Bat species, mass, and sex were recorded for all captures. I assessed age (juvenile or adult) based on the degree of ossification of the metacarpal-phalanx joints (Racey 1974) and female reproductive condition by abdominal palpation and inspecting mammae (Kunz 1988). I followed the guidelines of the American Society of Mammalogists for the capture, handling, and care of mammals (Animal Care and Use Committee 1998).

I used radio transmitters (Blackburn Transmitters, Nacogdoches, Texas, USA and Holohill Systems Limited, Ontario, Canada) to locate bats at their diurnal roost sites from mid-May until early August. Transmitters were bonded to the mid-scapular region with Skin-Bond® surgical adhesive following partial hair removal. Depending on the species of bat, individuals were instrumented with 0.24−0.71-g transmitters with 11−21-day batteries. Transmitter load was generally <5% of body mass (Aldridge and Brigham 1988). Bats were banded with a split-ring, numbered, plastic band on the forearm to aid in re-identification.

I tracked each bat to its roost site the morning following capture and approximately 5 days/week until its signal was lost. I used 5 15.3-m radiotelemetry towers (each equipped with 2 2-m, 13-element, high-gain yagi antennas) located on the highest elevations in the basin to determine general bat locations and hand-held yagi

antennas to locate exact roost locations (trees or snags). To ensure that locations of bats were accurate, bats were visually located either from the ground using binoculars and spotting scopes, or by climbing the tree. Because individual tree bats (especially those that roost in foliage) often roost at multiple roost sites (e.g., Menzel et al. 1998), instrumented bats were relocated as often as possible until their batteries failed or the transmitters were shed. Thus, I located multiple roosts for most individual bats. I collected Global Positioning System (GPS) coordinates for each bat location using Rockwell® PLGR GPS receivers (Rockwell-Collins, Cedar Rapids, Iowa, USA). Based on field observation, those units typically had an accuracy of ±10 m.

Vegetation mapping

Spatial analyses were conducted using both ArcMap® 3.2 and ArcView® 9.0 (Environmental Systems Research Institute, Redlands, California, USA). Vector maps of forest stand boundaries were obtained from the Ouachita National Forest. To more accurately reflect size and shape of forest stands, I redrew boundaries using a 10-m digital color orthoquad (DOQ) as a template. I classified Forest stands based on the Continuous Inventory and Stand Condition Management System (CISC) database that is maintained by the Fourche-Jessieville-Winona Ranger District of the ONF. Forest type, conditions, and past silvicultural treatments were ground-checked and corrected in the data layer, and tree-core data from most stands were used to verify stand ages. I digitized vegetative class boundaries for industrial timberlands from 10-m DOQs and classified habitats using ground-truthing.

Based on corrected CISC information, I classified each stand into 1 of 13 forest habitat classes (Table 1.1; Fig. 1.2). For stands that were primarily even-aged, habitat classifications were based on forest type (pine or hardwood) and age; otherwise, stands were classified based on silvicultural treatment. I differentiated hardwood and pine stands because some species of bat (e.g, Seminole bats) roost primarily in pines, whereas others (e.g., eastern red bats) roost primarily in hardwoods (Menzel et al. 1998). I differentiated stands by age because age in primarily even-aged stands is a major determinant of vertical structure and tree density (both indices of structural clutter) within forest stands (e.g., Baker et al. 1996). All age classes were based on ages of stands in the year 2000. I chose age classes based on stand successional stages presented by Baker et al. (1996) for pine types in the southeastern U.S. I derived the following age classes based on field observations of relationships between successional stage and age: stands <15 years old (stand initiation phase); stands 15−29 years old (early stem exclusion phase); stands 30−49 years old (late stem exclusion stage); stands 50−100 years old (understory reinitiation stage); and stands ≥100 years old (old growth stage). To reduce the number of classes included in the analysis, forest habitat classes that were available to only 1 or 2 species and that were <1% of available were removed from the analysis; those habitats included hardwood stands 15−29 and 30−49 years old.

In partially harvested stands on USFS lands, unharvested greenbelts could not be delineated from harvested portions using DOQs. Further, the vast number of those relatively small features made GPS unfeasible. Thus, habitat maps did not include greenbelts in partially harvested stands, but roosts located in greenbelts and on greenbelt

edges were recorded. Larger SMZs surrounding streams on industrial timberlands and USFS lands were classified as separate stands based on their age and timber type.

I used broad categories for forest type to reduce "fuzzy" edges that existed between adjacent stands that differed only slightly in pine or hardwood composition. Because older pine stands typically included a hardwood component, predominantly pine, pine-hardwood, and hardwood-pine stands were designated as mixed pine-hardwood for mature classes (≥50 years old). Pure hardwood forest types were designated simply as hardwood stands. Because of historical management in the basin, most even-aged stands <30 years old were pine with a limited hardwood component.

Because single-tree selection stands and pine-woodland restoration areas were in the early stages of development and were treated initially with similar partial harvesting, midstory removal, and burning in 2000, those 2 treatments were grouped into a "thinned mature" class. Industrial timberlands were managed using intensive even-aged management. Most of those lands were short-rotation, loblolly-pine plantations with little hardwood component. Thus, I used 3 habitat classes for industry plantations: young open clearcuts (approximately <10 years of age), closed canopy plantations (approximately 10−18 years of age), and older thinned plantations (approximately ≥19 years of age). No clearcuts <10 years old existed on USFS lands within the study area.

Analysis

Determining boundaries of "available" habitat is critical to the results of any resource selection study and available habitats must represent areas that are accessible to the animal (Aebischer et al. 1993, Alldredge et al. 1998). Instead of defining habitat

availability for all individuals in an arbitrarily delineated study area, I defined habitat availability for each individual separately, based on the location of their roosts. For each individual, I created a 1,000-m-radius polygon around each roost location for that individual and then combined all polygons to create the area of available habitat for that individual. I generated 200 random locations within that polygon to compare roost locations with random locations. Limited information is available on home-range sizes of forest bats in the southeastern U.S. Although the 1,000-m radius (314 ha) is less than average home range areas reported for big brown bats (2,906 ha; Brigham 1991), it corresponded roughly with the average maximum distance traveled by red bats during foraging in forested environments of the southeastern U.S. (Elmore et al. 2005), and the average distance (1,137 m) between roost locations and foraging areas for eastern pipistrelles (Krishon et al. 1997). Thus, selection estimates were at a similar scale as Johnson's (1980) third-order selection (selection of sites within an animal's home range).

I used Euclidean distance statistics (Conner and Plowman 2001) to compare random locations with locations of roosts. Distance grids were created for each forest habitat class in ARCGIS®, and the distance to each habitat class from each random and roost location was used for analysis. I then created a ratio of use for each forest habitat class by dividing the mean roost distance by the mean random location distance and standardizing that value by subtracting 1. Most individual bats had multiple roosts. Because individuals frequently roosted in different roosts within the same general area over multiple days, roost locations for individuals were not independent (Hurlbert 1984). To eliminate this spatial autocorrelation, I considered the individual bat as the experimental unit (Miller et al. 2003) by averaging the distances to each habitat for each

individual. I used separate MANOVA (PROC GLM; SAS Institute Inc. 2000) for each species of bat to determine if overall standardized ratios differed from 0. If the ratio was <0, the habitat was used more than expected; if the ratio was >0, the habitat was avoided. For each species, if MANOVA results indicated that an overall difference existed in proximity to the 13 habitat types between roost and random locations, I used *t*-tests to determine if individual habitats were preferred or avoided. I had sufficient numbers of individuals of each sex to compare habitat selection by gender for only eastern red and northern longear myotis. For those 2 species, I conducted MANOVA by sex and for both sexes combined. I used Hochberg sequential error controls for all univariate tests to maintain experiment-wise error rates (Wright 1992). I evaluated all tests at alpha = 0.10 to reduce the chance of committing Type 2 errors, the consequences of which may be as severe as the consequences of Type I errors (Toft and Shea 1983).

Because results of euclidean distance analysis may require substantial interpretation (Dussault et al. 2005, Conner et al. 2005), I calculated percentage of available habitat and percentage of roosts in each habitat class to aid in interpretation. To determine habitat availability for each species, I combined all 1,000-m polygons surrounding roost locations for that species into a single polygon and calculated percentage of each forest habitat class within this combined polygon. During the 6 years of study, industrial timberlands in the basin underwent harvest and thinning, which changed yearly proportions of young clearcuts, closed-canopy pine plantations, and thinned pine plantations. Therefore, I used a weighted average to represent proportional availability of those habitats during the entire study period. For each year, proportions of

those habitats were weighted by the proportion of total roosts located during that year; proportions of those 3 habitats were then averaged for the entire study period.

RESULTS

Over the 6 summers, I captured 715 bats during 344 net nights. I located 428 roosts from 162 individuals of 6 species: big brown, evening, northern longear myotis, eastern red, Seminole, and eastern pipistrelle. An additional 12 roosts of 9 hoary bats were not included in analyses because sample size was too small. I captured no adult female Seminole or evening bats in the basin during the period of summer under study. Total numbers of individuals included in the analysis were 16 big brown bats (12 males and 4 females), 17 male evening bats, 42 northern longear myotis (21 males and 21 females), 42 red bats (22 males and 20 females), 28 eastern pipistrelle bats (21 males and 7 females), and 17 male Seminole bats. Average number of roosts obtained for each individual was 2.1 (SE = 0.3; range 1−5) for big brown bats, 2.6 (SE = 0.5; range 1−8) for evening bats, 2.4 (SE = 0.2; range 1−7) for northern longear myotis, 3.5 (SE = 0.3; range 1−9) for eastern red bats, 1.8 (SE = 0.2; range 1−5) for eastern pipistrelles, and 3.0 (SE = 0.4; range 1−6) for Seminole bats. For the 2 species with sample sizes large enough to analyze by sex, I obtained 72 male and 73 female roosts for eastern red bats and 55 male and 47 female roosts for northern longear myotis. Overall MANOVA results indicated selection occurred among the 13 forest habitat classes for each of the 6 bat species.

Cavity- and crevice-roosting species

Big brown bats−Mean distances to 13 forest habitat classes differed between roost and random locations for combined sexes of big brown bats (Wilk's $\lambda = 0.008$, $F = 26.97$, *d.f.* = 13, 3; $P = 0.010$). Big brown roosts were associated with thinned mature (recently cut pine woodland areas and single-tree selection stands collectively) and mixed pine-hardwood ≥100 years old (Table 1.2); no habitats were avoided. The majority (52.9%) of big brown roosts were in thinned mature habitats, followed by group selection (26.5%; Table 1.3). In those 2 habitats, 11% of roosts in thinned mature stands were located in unharvested greenbelts or greenbelt edges, and 22% of roosts in group selection were in greenbelts.

Evening bats− Mean distances to 13 forest habitat classes differed between roost and random locations for male evening bats (Wilk's $\lambda = 0.043$, $F = 6.87$, *d.f.* = 13, 4; $P = 0.038$). Roosts of male evening bats were closer than random locations to thinned mature and mixed pine-hardwood ≥100 years old; no habitats were avoided (Table 1.2). Most (57.4%) roosts were located in thinned mature, whereas 36.1% of roosts were in mixed pine-hardwood and hardwood 50−99 years old that had not been harvested or thinned (Table 1.3). In thinned mature stands, 48.1% of roosts were located in unharvested greenbelts or greenbelt edges, and 66.7% of roosts in group selection were located in those areas.

Northern longear myotis−Mean distances to 13 forest habitat classes differed between roost and random locations for combined sexes of northern longear myotis (Wilk's $\lambda = 0.178$, $F = 10.31$, *d.f.* = 13, 29; $P < 0.001$). Roosts of that species were associated with thinned mature, pine seed-tree stands, and hardwood or mixed pine-

hardwood ≥100 years old; no forest habitat class was avoided (Table 1.2). Most (57.4%) roosts were located in thinned mature habitats, followed by mixed pine-hardwood 50−99 years old (22.5%), and group-selection (17.6%; Table 1.3).

When analyzed by sex, mean distances to 13 forest habitat classes differed between roost and random locations for female northern longear myotis (Wilk's λ = 0.073, F = 7.78, d.f. = 13, 8; P = 0.003). Females roosted significantly closer to thinned mature ($P < 0.001$), pine-hardwood ≥100 years old (P = 0.001), hardwood ≥100 years old (P = 0.002), and group-selection (P = 0.017) than random. No habitats were significantly avoided by females. For females, roosts were located in the following habitats: thinned mature (57.4%), mixed pine-hardwood 50−99 years old (21.3%), group selection (17.0%), hardwood 50−99 years old (2.1%), and pine 30−49 years old (2.1%). For the 2 partially harvested habitat classes 22.2% of roosts in thinned mature were located in greenbelts or greenbelt edges, and 37.5% of roosts in group-selection were located in those unharvested buffers.

Mean distances to 13 forest habitat classes differed between roost and random locations for male northern longear myotis also (Wilk's λ = 0.113, F = 4.85, *d.f.* = 13, 8; $P < 0.016$). Males roosted closer to thinned mature ($P < 0.001$), pine-hardwood ≥100 years old (P = 0.014), and seed-tree stands (P = 0.016) than random; no forest habitat class was significantly avoided by males. For males, roosts were located in the following habitats: thinned mature (41.8%), mixed pine-hardwood 50−99 years old (23.6%), group selection (18.2%), hardwood 50−99 years old (5.5%), mixed pine-hardwood ≥100 years old (5.5%), hardwood ≥100 years old (1.8%), closed canopy loblolly plantations (1.8%), and thinned loblolly plantations (1.8%). For the 2 partially harvested habitats, 47.8% of

roosts in thinned mature stands were located in greenbelts or greenbelt edges, and 30.0% of roosts in group-selection were located in those unharvested buffers.

Vegetation-roosting species

Eastern red bats−Mean distances to 13 forest habitat classes differed between roost and random locations for combined genders of red bats (Wilk's $\lambda = 0.13$, $F = 14.92$, *d.f.* = 13, 29; $P < 0.001$). Red bat roosts for both sexes combined were closer than random locations to thinned mature, group selection, and hardwood ≥100 years old; no habitat classes were avoided (Table 1.2). For both sexes combined, most (28.3%) roosts were in thinned mature habitats, followed by mixed pine-hardwood 50−99 years old (24.8%), and hardwood 50−99 years old (15.2%; Table 1.3).

When analyzed by gender, mean distances to 13 forest habitat classes differed between roost and random locations for female red bats (Wilk's $\lambda = 0.058$, $F = 8.69$, *d.f.* = 13, 7; $P = 0.004$) Females roosted significantly closer to thinned mature ($P < 0.001$) and pine-hardwood 50−99 years old ($P = 0.043$) than random; no habitats were significantly avoided by female red bats. Female roosts were located in the following habitats: mixed pine-hardwood 50−99 years old (28.8%), thinned mature (21.9%), group selection (17.8%), hardwood ≥100 years old (12.3%), hardwood 50−99 years old (11.0%), older thinned loblolly pine plantations (6.8%), and closed-canopy loblolly plantation (1.4%). For the 2 partially harvested habitats, 62.5% of female roosts in thinned mature stands were located in greenbelts or greenbelt edges, and 53.8% of roosts in group-selection stands were located in those unharvested buffers.

Mean distances to 13 forest habitat classes differed between roost and random locations for male red bats as well (Wilk's $\lambda = 0.086$, $F = 7.34$, *d.f.* = 13, 9; $P = 0.003$). Male red bats roosted significantly closer to group-selection ($P = 0.007$) and pine-hardwood 50−99 years old ($P = 0.0261$) than random; males significantly avoided pine 30-49 years old ($P = 0.024$). Male red bat roosts were located in the following habitats: thinned mature (34.7%), mixed pine-hardwood 50−99 years old (20.8%), hardwood 50−99 years old (19.4%), group selection (9.7%), mixed pine-hardwood ≥100 years old (5.6%), hardwood ≥100 years old (4.2%), pine 15−29 years old (4.2%), and closed-canopy loblolly plantation (1.4%). For the 2 partially harvested habitats, 36.0% of male roosts in thinned mature stands were located in greenbelts or greenbelt edges, and 57.1% of roosts in group-selection stands were located in those unharvested buffers.

Seminole bats−Mean distances to 13 forest habitat classes differed between roost and random locations for male Seminole bats (Wilk's $\lambda = 0.004$, $F = 69.26$, *d.f.* = 13, 4; $P = 0.0005$). Roosts of male Seminole bats were closer than random to thinned mature (Table 1.2). That species avoided hardwood or mixed pine-hardwood 50−99 years old and pine 15−29 years old. Most (60.8%) Seminole roosts were in thinned mature habitats (Table 1.3). Only 15% of Seminole roosts were located in stands that were not partially harvested or thinned. For the 2 partially harvested habitat classes, only 1 roost was located in a greenbelt, all other roosts in those stands were located in harvested portions of stands.

Eastern pipistrelles−Mean distances to 13 forest habitat classes differed between roost and random locations for combined sexes of eastern pipistrelles (Wilk's $\lambda = 0.35$, $F = 31.49$, *d.f.* = 13, 15; $P < 0.001$). Eastern pipistrelles roosted closer than random to

group selection, pine seed-trees, mixed pine-hardwood ≥ 100 years old, hardwood 50−99 years old, and closed-canopy loblolly pine plantations; no forest habitat class was significantly avoided (Table 1.2). Most (65.3%) pipistrelle roosts were in hardwood or mixed pine-hardwood stands ≥50 years of age. Although 34.7% of roosts were located in partially harvested stands (Table 1.3), 90.0% of roosts in thinned mature and 85.7% of roosts in group selection were in greenbelts or greenbelt edges.

All bat species

Based on availability to all bat species, the most abundant habitat class was thinned mature (average of 22.8% of available habitat among all species), followed by unharvested mixed pine-hardwood 50−99 years old (22.4%), and group selection (11.8%; Table 1.3). The habitat containing the most roosts was thinned mature (41.3% of roosts were located in this habitat class), followed by mixed pine-hardwood forest 50−99 years old (19.9% of roosts), and group selection (14.7% of roosts). No roosts were located in pine seed-trees or recent clearcuts. Based on analyses of Euclidean distances, the most preferred habitat class among all 6 species was thinned mature (Table 1.2). Distances for 5 of 6 species were significantly less than random for this habitat. The second most preferred habitat class was mixed pine-hardwood forest ≥100 years old; 4 bat species roosted closer to that habitat class than random. However, that habitat comprised only an average of only 3.5% of the available habitat. Mixed pine-hardwood 50−99 years old was the second most abundant habitat class available, and the second most used habitat (19.9% of roosts), but distance statistics indicated it was preferred only by red bats when sexes were analyzed separately. Recently harvested group selection stands were the third

most used stands (14.7% of roosts), and 2 bat species (5 if experiment-wise error controls had not been applied) preferred that habitat class based on distance statistics.

DISCUSSION

Consistent with predictions 1 and 2, bats generally selected areas for roosting with relatively low tree density but contained abundant mature trees. Five of the 6 species preferred to roost in close proximity to mature mixed pine-hardwood forest that had undergone recent partial harvesting and midstory removal, and 41.3% of roosts were located in that habitat class. Those areas were relatively open, had little or no midstory, and contained mature pines, mature hardwoods, and abundant snags. Studies suggest many species of bats prefer to roost in stands with low tree density (Hutchinson and Lacki 2000, Menzel et al. 2001), low canopy coverage (Sasse 1995, Vonhof and Barclay 1996, Brigham et al. 1997a), and little understory vegetation (Menzel et al. 2001, Menzel et al. 2002a). For example, Cambell et al. (1996) found that roost sites had less canopy closure, lower understory density, and lower understory height compared with random areas, and Elmore et al. (2004) found that red bats roosted most often in thinned loblolly pine plantations in an area dominated by industrial timberlands. The open forest conditions of thinned mature stands may have approximated historical forest conditions. Oak and pine woodlands maintained by periodic fire, with open overstories and primarily herbaceous understories, were once abundant throughout the southeastern U.S. and the Ozark and Ouachita Mountain physiographic region but are now limited to a few areas that have been recently restored (Masters et al. 1995, Lorimar 2001).

Partially harvested stands (pine woodland restoration areas, single-tree selection, and group-selection stands) were not spatially homogeneous. Most of these stands contained abundant greenbelts. In partially harvested stands, 88.0% of eastern pipistrelle roosts, 49.2% of eastern red roosts, and 50.0% of male evening bat roosts were in greenbelts. Alternatively, only 14.8% of big brown and 2.7% of Seminole roosts in those stands were in greenbelts. Thus, some species relied heavily on greenbelts in partially harvested stands and other species rarely used them for roosting. Because greenbelts were primarily around ephemeral drains that did not hold water except during heavy rain events, use of those areas likely was attributed to their structure and placement in the landscape. Abundant substrate (including snags) and adjacency to open habitats may have made greenbelts attractive roost sites for some species. Greenbelts appear to be important landscape features to eastern pipistrelles, and to a lesser extent, red bats and male evening bats. If greenbelts had not been present, the extent of roosting by those 3 species in partially harvested stands is unclear. Nonetheless, results suggest that spatially heterogeneous areas may be important to the roosting ecology of some species.

Favorable conditions for roosting that were created immediately after partial harvesting and midstory removal are likely ephemeral. The majority of partial harvesting and group selection harvesting in the basin was conducted in winter 1999−2000. For the single-tree selection and group-selection stands, that harvest was the first entry into the stands. The goal of most single-tree selection management is to maintain ≥3 distinct age classes of trees within a stand (Baker et al. 1996). Further, group-selection management involves creating new group openings approximately every 10 years, which leads to spatial heterogeneity throughout the stand. Over time, the single-tree selection and

group-selection stands will likely increase in clutter and tree density as additional cohorts of trees regenerate; these stands may become more cluttered than mature, second-growth, even-aged stands in the long term. However, little information is available on the long-term effects of these treatments on roost selection by forest bats. Pine woodland restoration areas, with their open, park-like conditions, are maintained via periodic burning and will likely provide sustainable open habitats with abundant mature trees for roosting through the future as long as important substrates such as overstory hardwoods and snags remain available.

Although mature, generally even-aged, mixed pine-hardwood forest 50−99 years of age was the second most abundant habitat available to bats (22.4%), distance statistics indicated only red bats (when genders were analyzed separately) preferred that habitat. Hardwood forests in that age class were preferred by eastern pipistrelles. Both of those habitat classes were avoided by Seminole bats. Both mixed pine-hardwood and hardwood stands 50−99 years old consisted of second-growth forests that received little or no silvicultural treatments and were moderately cluttered with midstory trees. Unmanaged, second-growth forests such as those are abundant throughout the eastern and southeastern U. S. and likely do not represent optimal roosting habitat for species such as Seminole bats. Old-growth (≥ 100 years old) pine-hardwood stands were preferred by 4 of 6 bat species, and old-growth hardwood stands were preferred by 2 species. Those results were consistent with studies that indicated many bats species prefer older forest stands (e.g., Thomas 1988).

Few differences existed among habitat preferences for the 3 cavity- and crevice-roosting species. All preferred recently thinned mixed pine-hardwood forest and old-

growth pine-hardwood forest, although male evening bats tended to use unharvested greenbelts in partially harvested areas more than the other 2 species. Northern longear myotis were associated with old-growth hardwoods and seed-tree cuts, whereas the other 2 species were not. All 3 species rely to some extent on snags for roosting. Snags were the substrate for 100% of big brown, 89% of northern longear myotis, and 58% of male evening bat roosts. Regardless of stand structure, abundance of these cavity-roosting species may be limited by presence of adequate numbers of snags (Brigham et al. 1997a). Different forest habitat classes may have differed in abundances of large snags. For example, snag densities in South Carolina were highest in hardwood forest types and lowest in pine plantations; intermediate age classes had higher snag densities than older or younger stands of the same type (Moorman et al. 1999). A wide-spread ice storm in the study area during winter 2000−2001 created abundant pine, and to a lesser extent hardwood, snags throughout the basin. Hardwood snag creation also was included in the harvest prescriptions for single-tree selection and pine woodland restoration areas. Thus, it was unlikely that most habitat classes lacked abundant snags. Nevertheless, without these disturbances, some of the preferred habitats may have not had adequate densities of snags to support roosting by those 3 species. Long-term snag dynamics under different silvicultural systems in the southeastern U.S. are unknown, and future research should address snag sustainability under different silvicultural systems.

There appeared to be segregation in roosting habitat among vegetation-roosting species. Male Seminole bats were associated primarily with open stands that had been partially harvested or thinned and contained overstory pines; that species rarely roosted in hardwood or relatively dense stands. My results indicate that Seminole bats (at least

males) prefer to roost in relatively open habitats with mature pines, suggesting they may have evolved to use the vast pine woodlands that were historically abundant across the southeastern U.S. (Lorimar 2001). In contrast, eastern pipistrelles tended to roost in stands that were more structurally complex, with higher overstory tree densities and abundant midstory hardwoods. In group-selection and thinned mature stands, their roosts were usually in unharvested greenbelts that were more structurally cluttered than the surrounding treated stand. Red bats selected both thinned stands and unharvested stands that contained mature overstory hardwoods. In partially harvested stands, they frequently roosted in both greenbelts and the harvested portions of the stands. Red bats are likely habitat generalists, and select stands based on the presence of overstory hardwoods. However, Elmore et al. (2004) found red bats frequently roosted in pines in a landscape dominated by thinned pine plantations.

Consistent with prediction 3, Euclidean-distance statistics suggested eastern pipistrelles and male northern longear myotis preferred to roost in closer proximity to recent seed-tree cuts than random locations, but no roosts were located in this habitat class. Roosts of both species were frequently located in habitats adjacent to seed-trees. Seed-tree cuts were open habitats with no large hardwoods and only scattered pines. Thus, those areas provided little roosting structure. Seed-tree cuts were located primarily in areas of the basin where little other harvesting was conducted. Thus, open habitats were rare in those areas and seed-tree cuts offered open habitats for foraging. Openings in areas of continuous forest are frequently used for foraging by bats and bats may prefer to forage in those areas (Burford and Lacki 1995, Grindal and Brigham 1998, Menzel et al. 2002b, Owen et al. 2004). Although research suggests that eastern pipistrelles are

adapted for foraging in cluttered habitats (Menzel et al. 2005), their activity was greatest in clearcuts and open areas in Georgia (Menzel et al. 2003). Therefore, pipistrelles and northern longear myotis may have roosted in close proximity to these areas to reduce energetic costs associated with flights to foraging areas.

Distance ratios indicated that eastern pipistrelles roosted closer to closed-canopy loblolly pine plantations than random, but none roosted in that habitat. Closed-canopy plantations were likely the least usable habitats for roosting in the basin. Closed-canopy plantations were virtually impenetrable to bats; they were dense and cluttered, with high BAs, few hardwoods, and no large snags. Among all 6 species, only 3 individual bats (2 red and 1 northern longear myotis) roosted within those stands, and both red bats roosted in small groups of imbedded hardwoods within the plantations. Bats of all species that were captured and instrumented in SMZs located within closed-canopy plantations typically roosted around the periphery of those plantations in adjacent habitats, and several roosts were located within sight of these plantations. The association between bats and this habitat class may have been an edge effect. Many bat species tend to forage and commute in edge habitats (Ekman and de Jong 1996, Grindal and Brigham 1999, Verboom and Spoelstra 1999, Hogberg et al. 2002), and boundaries between those plantations and adjacent stands provided the hardest edges in the study area.

My results suggesting that bats preferred seed-tree cuts and closed canopy pine plantations are consistent with potential problems associated with DA that were pointed out by Dussault et al. (2005). Their critique suggested that use of DA can result in a habitat being preferred even though animals never used that habitat. However, Conner et al. (2005) suggested that this analysis yields insights into associations that would be

otherwise overlooked with classification-based analysis. I contend that the results of DA are not always straightforward; however, results can be interpreted with a thorough knowledge of both the biology of the species in question and a detailed knowledge of the data.

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Table 1.1. Forest habitat classes used to compare habitat selection of 6 bat species during diurnal summer roosting in the Ouachita Mountains of west-central Arkansas, 2000−2005.

Habitat class	Description
Pine <15 yrs	Even-aged pines, <15 years old
Pine 15−29 yrs	Even aged pines, 15−29 years old
Mixed P/H 30−49 yrs.	Primarily pine with a hardwood component, generally even-aged, 30−49 years old
Mixed P/H 50−99 yrs.	Mixed pine and hardwood stands, primarily even-aged, 50−99 years old. No history of thinning, few controlled burns
Mixed P/H ≥100 yrs.	Mixed pine and hardwood stands, ≥100 years old. No history of thinning and ≤1 known controlled burns
Hardwood 50−99 yrs.	Hardwood stands, primarily even-aged, 50−99 year old. No history of thinning, few controlled burns
Hardwood ≥100 yrs.	Hardwood stands ≥100 years old. No history of thinning and ≤1 known controlled burns
P/H group selection	Mature mixed pine-hardwood stands that had undergone mostly recent group selection harvest and matrix thinning
P/H thinned mature	Mature (> 50 years old) mixed pine-hardwood stands that had undergone recent partial overstory reduction and midstory removal; included single-tree selection stands and pine

Table 1.1 − continued.

Habitat class	Description
	woodland restoration areas in the early stages of transition to desired future conditions
Pine seed-tree	Seed-tree cuts, open stands with scattered mature pines left for seed production
Closed plantation	Closed-canopy loblolly pine plantations, approximately 14−25 years of age
Thinned plantation	Older/thinned loblolly pine plantations, approximately 20−35 years of age
Clearcut	Young, recently harvested (< 3 years old) industrial clearcuts

Table 1.2. Mean Euclidean distance ratios for roosting habitat selection among 13 forest habitat classes and *t*-test probability values comparing mean ratios with a value of 0 for 6 species of bats in the Ouachita Mountains of west-central Arkansas, 2000−2005.

	Big Brown[a] (n = 16)[c]		Evening[b] (n = 17)		N. Longear Myotis[a] (n = 42)		Red[a] (n = 42)		Seminole[b] (n = 17)		E. pipistrelle[a] (n = 28)	
Habitat	Mean	P > |t|	Mean	P > |t|	Mean	P > |t|	Mean	P > |t|	Mean	P > |t|	Mean	P > |t|
Pine <15 yrs.	-0.005[d]	0.913	0.019	0.736	-0.010	0.790	-0.009	0.796	0.064	0.273	0.040	0.437
Pine 15−29 yrs.	-0.134	0.147	-0.081	0.328	-0.004	0.915	0.003	0.961	0.142	*0.011	0.068	0.240
Mixed P/H 30−49 yrs.	-0.001	0.983	0.049	0.313	-0.060	0.177	0.060	0.072	-0.114	0.124	0.029	0.408
Mixed P/H 50−99 yrs.	-0.123	0.452	-0.049	0.780	-0.110	0.215	-0.067	0.429	0.139	*0.012	-0.182	0.045
Mixed P/H ≥100	-0.256	*0.007	-0.165	*0.021	-0.193	*0.000	-0.055	0.249	-0.195	0.021	-0.311	*0.000
Hardwood 50−99 yrs.	0.088	0.360	0.035	0.892	-0.107	0.159	-0.090	0.316	0.139	*0.012	-0.357	*0.000
Hardwood ≥100 yrs.	-0.042	0.127	-0.005	0.788	-0.032	*0.000	-0.086	*0.020	-0.035	0.175	0.013	0.485
P/H Group selection	-0.184	0.091	-0.089	0.265	-0.151	0.056	-0.252	*0.000	-0.232	0.050	-0.227	*0.012
P/H thinned mature	-0.584	*0.000	-0.657	*0.000	-0.506	*0.000	-0.307	*0.000	-0.599	*0.000	-0.175	0.149

Table 1.2. –continued.

Habitat	Big Brown[a] (n = 16)[c]		Evening[b] (n = 17)		N. Longear Myotis[a] (n = 42)		Red[a] (n = 42)		Seminole[b] (n = 17)		E. pipistrelle[a] (n = 28)	
	Mean	P > |t|	Mean	P > |t|	Mean	P > |t|	Mean	P > |t|	Mean	P > |t|	Mean	P > |t|
Pine seed-tree	-0.078[d]	0.057	-0.079	0.072	-0.089	*0.000	0.001	0.910	-0.032	0.574	-0.024	*0.000
Closed plantation	-0.017	0.729	-0.105	0.091	-0.068	0.037	-0.068	0.048	0.011	0.569	-0.173	*0.000
Thinned plantation	-0.018	0.449	-0.103	0.240	-0.011	0.697	-0.043	0.266	-0.055	0.543	-0.134	0.065
Clearcut	0.003	0.821	-0.011	0.334	-0.010	0.349	0.009	0.349	-0.011	0.610	-0.034	0.151

[a] Both sexes combined.

[b] Males only

[c] Number of individuals included in the analysis.

[d] Distance ratios = (mean distance from roost to habitat/mean distance from random location to habitat) - 1; values <0 (negative) indicate roosts were closer to a habitat than random, values >0 (positive) indicate roosts were further from a habitat than random.

* Significant at the 0.10-level with Hochberg adjustment for experiment-wise error control.

Table 1.3. Percentage of available habitat in 13 forest habitat classes and percent of roosts in each class for 6 species of forest bats in the Ouachita Mountains of west-central Arkansas, 2000−2005.

	Big Brown[a] (n = 34)[c]		Evening[b] (n = 47)		N. Longear Myotis[a] (n = 102)		Red[a] (n = 145)		Seminole[b] (n = 51)		E. pipistrelle[a] (n = 49)	
Habitat	Avail.	Roost	Avail.	Roost	Avail.	Roost	Avail.	Roost	Avail.	Roost	Avail.	Roost
Pine <15 yrs.	2.3	0	6.1	0	4.4	0	3.3	0	7.0	0	3.1	0
Pine 15−29 yrs.	5.1	0	6.6	0	5.2	0	7.9	2.1	10.7	0	10.6	0
Mixed P/H 30−49 yrs.	2.2	0	6.0	0	3.0	1.0	4.8	0	10.6	2.0	5.2	0
Mixed P/H 50−99 yrs.	19.7	14.7	19.0	19.1	21.8	22.5	24.4	24.8	30.5	2.0	18.8	22.4
Mixed P/H ≥100	5.3	5.9	2.6	0	3.6	2.9	2.8	2.8	1.6	11.8	5.0	8.2
Hardwood 50−99 yrs.	5.6	0	6.8	17.0	10.5	3.9	12.7	15.2	4.9	0	9.6	34.7
Hardwood ≥100 yrs.	0	0	0.1	0	0.4	1.0	3.1	8.3	5.5	0	0.0	0
P/H Group selection	16.1	26.5	7.1	6.4	15.7	17.6	13.4	13.8	8.0	11.8	11.0	14.3

Table 1.3. –continued.

Habitat	Big Brown[a] (n = 34)[c]		Evening[b] (n = 47)		N. Longear Myotis[a] (n = 102)		Red[a] (n = 142)		Seminole[b] (n = 51)		E. pipistrelle[a] (n = 49)	
	Avail.	Roost	Avail.	Roost	Avail.	Roost	Avail.	Roost	Avail.	Roost	Avail.	Roost
P/H thinned mature	38.5	52.9	26.3	57.4	20.7	49.0	16.8	28.3	9.6	60.8	24.6	20.4
Pine seed-tree	1.6	0	2.9	0	1.8	0	1.0	0	3.4	0	1.6	0
Closed plantation	2.2	0	13.1	0	10.0	1.0	5.6	1.4	3.4	0	6.5	0
Thinned plantation	1.3	0	3.0	0	2.6	1.0	4.0	3.4	3.6	11.8	2.6	0
Clearcut	0.1	0	0.5	0	0.4	0	0.3	0	1.3	0	1.4	0

[a] Both sexes combined.

[b] Males only

[c] Number of roosts included in the analysis.

Fig. 1.1. Location and topography of the study area (Winona Basin) within the Ouachita Mountains of west-central Arkansas.

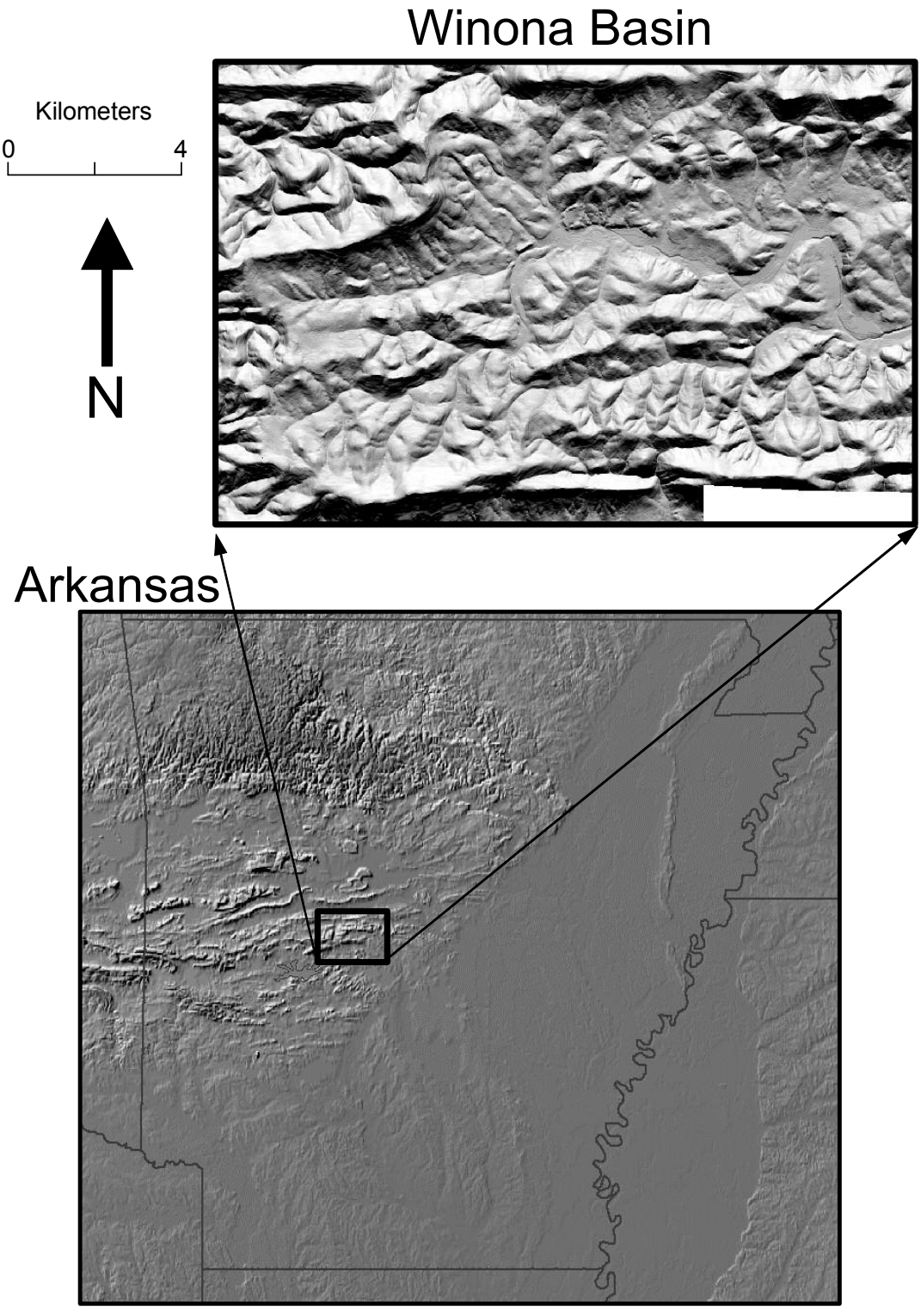
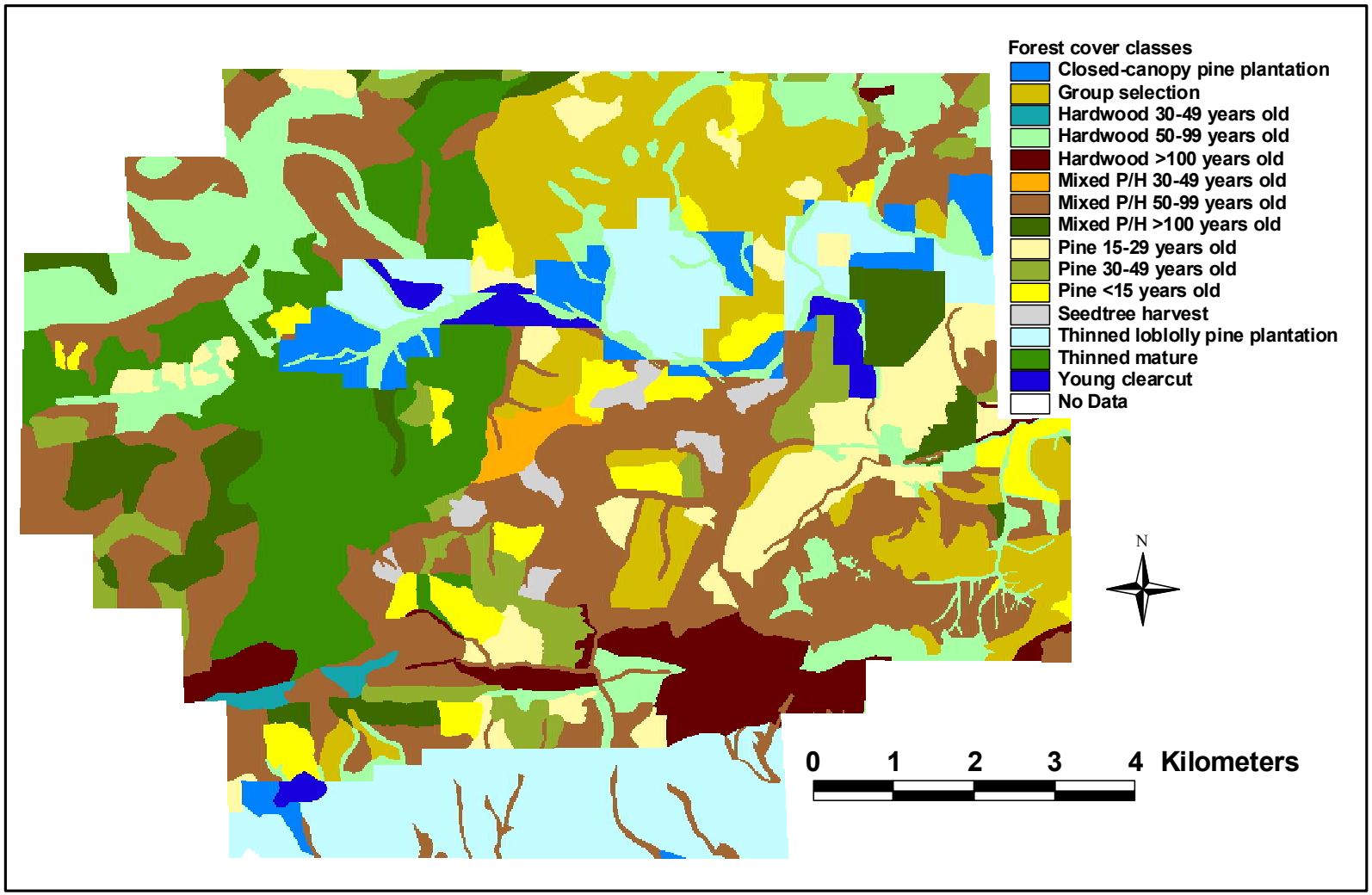

Winona Basin
Kilometers
0
4
N
Arkansas

Fig. 1.2. Forest habitat classes of the Winona Basin and surrounding area.


Forest cover classes
Closed-canopy pine plantation
Group selection
Hardwood 30-49 years old
Hardwood 50-99 years old
Hardwood >100 years old
Mixed P/H 30-49 years old
Mixed P/H 50-99 years old
Mixed P/H >100 years old
Pine 15-29 years old
Pine 30-49 years old
Pine <15 years old
Seedtree harvest
Thinned loblolly pine plantation
Thinned mature
Young clearcut
No Data
N
0 1 2 3 4 Kilometers

CHAPTER 2

EFFECTS OF LANDSCAPE STRUCTURE AND COMPOSITION ON ROOST SELECTION BY A FOREST BAT COMMUNITY

Abstract. Although information exists on relationships between forest microhabitat and selection of roosts by forest-dwelling bats, little is known regarding effects of landscape arrangement on roost selection. Land managers also need to know how these landscape attributes and the characteristics of forest stands interact to affect selection of roosts. I evaluated effects of topography, forest habitat class, and landscape patch configuration on selection of summer roosts by 6 species of forest bats in a diverse forested landscape of west-central Arkansas to determine attributes of landscapes that were important in predicting occurrence of bat roosts. I modeled roost selection at 2 spatial extents to determine if the effects of landscape attributes were resilient to changes in spatial scale. In general, small-extent (a 250-m radius) models of landscape attributes associated with roost selection were a better fit than large-extent (1,000-m radius) models. For most of the 6 species, forest habitat class was more important than patch configuration or topography in differentiating roost from random locations regardless of extent. Topographic measurements were included in models more often than patch-configuration metrics. Most species roosted in areas that contained substantial amounts of recent partially harvested or thinned forest that retained a component of mature overstory trees. At both extents, eastern red bats (*Lasiurus borealis*) were more likely to roost in close proximity to roads, whereas eastern pipistrelles (*Pipistrellus subflavus*) were more likely to roost further from roads than random. Models for all bat species combined indicated

bats were more likely to roost in close proximity to water sources in areas with little relatively dense or young forest. Selection of roosts by forest bats was more influenced by forest-stand characteristics and proximity to water sources than patch-configuration metrics.

INTRODUCTION

Bats spend >50% of their time roosting, and roost sites play an important role in thermoregulation and protection from predators (Brigham et al. 1997a). Roost-site characteristics undoubtedly influence bat fitness and survival, and availability of adequate roost sites may limit numbers and distribution of certain species (Humphrey 1975, Vonhof and Barclay 1996). Studies suggest that forest management should be used to ensure that forests provide adequate roosting sites for bats (Brigham et al. 1997a, Crampton and Barclay 1998, Rabe et al. 1998). By manipulating age of forest stands, tree density, understory and midstory condition, and creating snags, land managers can provide more favorable forest structure within individual stands for roosting. However, if attributes of the surrounding landscape are as important as characteristics of forest stands, land managers need to know how landscape attributes and stand management interact to affect roost selection by forest bats.

Substantial research has been conducted on effects of patch arrangement, patch size, edges, matrix elements, fragmentation, and patch isolation on breeding birds and small mammals (e.g., Robbins et al. 1989, Barrett and Peles 1999, Villard et al. 1999, Rodewald and Yahner 2001). Recently, researchers have begun to study effects of patch arrangement and topographic features on activity and abundance of bats (e.g., Gehrt and

Chelsvig 2003, Gorrensen and Willig 2004), but only limited information exists on effects of those metrics on roost selection by bats in forested environments. Nonetheless, amount of edge, stand shapes and juxtapositions, elevations, and distance to roads or water sources could affect whether bats choose to roost at a particular site regardless of whether forest structure is adequate.

Effects of some topographic measurements (e.g., slope, elevation, and distance to streams) on roost selection by forest bats have been examined (Rabe et al. 1998, Cryan et al. 2000). For example, roost snags used by eight species of bat were often located near ridge tops and were closer to water than random snags in one study area in Arizona, and roosts of long-eared myotis (*Myotis evotis*) were more often located in upslope habitats (Rabe et al. 1998, Waldien et al. 2000). However, no studies have examined effects of patch configuration, topographic features, and forest-stand conditions concurrently on selection of roosts by forest bats.

Conclusions of many roost-selection studies also have been limited by lack of habitat and topographic diversity in the study area. If diverse habitats are not available for roost selection, conclusions about habitat selection may be misleading. For example, Hutchinson and Lacki (2000) quantified red bat (*Lasiurus borealis*) roosting in an area of continuous hardwood (deciduous broadleaf) forest "undisturbed by silviculture," and Elmore et al. (2004) quantified roosting on industrial timberlands comprised primarily of pine (*Pinus* spp.) plantations. Thus, true measurements of habitat preference are limited if a wide array of habitats are not available to the species under study. A diverse landscape allows the evaluation of a species' preferences across a wide array of habitats

and landscape attributes which can provide a better understanding of habitats that may be important.

My objectives were to evaluate effects of topography, forest habitat class, and landscape structure concurrently on selection of roosts by forest bats in a diverse forested landscape to determine attributes of landscapes that are potentially important in predicting occurrence of diurnal summer roosts. I created logistic regression models to differentiate areas selected for roosting from random areas for six species and modeled these responses at two spatial extents to determine if these relationships are resilient to changes in scale. Based on published literature, I developed the following predictions: 1) bats prefer to roost in habitats that are relatively less cluttered (Brigham et al 1997b, Mackey and Barclay 1989), with lower tree densities and reduced midstory (Sasse 1995, Campbell et al. 1996, Hutchinson and Lacki 2000); 2) bats prefer to roost in close proximity to travel corridors and foraging areas such as streams and roads (Walsh and Harris 1996, Grindal and Brigham 1998, Kalcounis-Ruppell et al. 2005); and 3) roost selection is influenced more by the attributes of specific habitat types than patch configuration metrics (Krusic et al. 1996, Zimmerman and Glanz 2000, Gehrt and Chelsvig 2003).

METHODS

Study area

The study was conducted in the 6,545-ha Upper Lake Winona Basin, situated in the Ouachita Mountains of west-central Arkansas (34°48'N, 92°58'W). The Ouachita Mountains consist of east-west oriented ridges with elevations of 152−853 m, mean

annual precipitation of 112−137 cm, and mean annual temperatures of 13.9−16.1 ^{o}C (Skiles 1981).

No residential areas, farms, houses, agricultural lands, or pastures existed in the study portion of the basin. Most of the basin consisted of mixed shortleaf pine (*P. echinata*)–hardwood forests managed by the U.S. Forest Service (Ouachita National Forest; ONF). The basin also contained a mix of other forest types including oak (*Quercus* spp.)–hickory (*Carya* spp.) and riparian hardwood forests. Twelve percent (778 ha) of the area was intensively managed industrial timberlands (owned by Weyerhaeuser Company). Those lands consisted primarily of closed-canopy and thinned loblolly pine (*P. taeda*) plantations managed under a 30–35-year rotation. Industrial plantations generally were thinned and pruned at 15−20 years of age. Industrial timberlands contained abundant unharvested buffer strips (streamside management zones; SMZ) established around streams for water-quality protection; those buffers typically were mature (>50 years old) hardwood forest.

National forest lands within the basin were divided into six 513−1,791-ha management units where different silvicultural treatments were implemented in 2000. A 1,232-ha shortleaf pine-woodland restoration unit was initially thinned and burned in 2000; the long-term goal of that management was to obtain an open woodland condition with an abundant herbaceous understory that is maintained by frequent prescribed burns (3−5 years). That area was thinned to 13.8 m^2/ha overstory basal area (BA); 1.1 m^2/ha of the total overstory BA was retained hardwoods. A 864-ha single-tree selection unit also was thinned to 13.8 m^2/ha of overstory BA, with 2.3 m^2/ha of the total overstory BA being hardwoods. Both treatments underwent partial midstory removal, whereby most

hardwoods <15 cm were felled. A 531-ha small group selection unit (openings of 0.4–0.81 ha) and a 513-ha large group selection unit (openings of 2.02–4.05 ha) consisted of thinned forest with patches of trees removed to create openings in the forest canopy. Openings retained about 2.3 m^2/ha of overstory BA (primarily pine). A 1,791-ha unit was managed using a mix of treatments and silvicultural systems, including single-tree selection and seedtree cuts (all trees were removed except for about 2.3 m^2/ha BA of mature pines left to produce seed for regeneration) in stands of about 16−18 ha. The basin also contained an 836-ha, mostly natural block, consisting primarily of mature, second-growth, pine-hardwood timber. Throughout the basin, stands (16−90 ha) that were either inoperable (e.g. slopes > 35%), in regeneration (typically <50 years of age), uneconomical to harvest, or dominated by uneconomical species such as hardwoods were interspersed within these treatment units. Thus, with its diversity of slopes, aspects, ownership, and treatment history the basin contained most of the predominant forest types, aspects, and forest-management practices that existed in the Ouachita Mountains.

Bat capture and radiotelemetry

From mid-May to early August 2000−2005, I captured bats between 2100 and 0130 CST at 21 trapping locations distributed throughout the basin. I trapped bats for 125 nights using 3−8 mist nets (2.6−12.0 m wide x 2.6 m tall). Trapping locations were primarily stream pools but included forest roads, ponds, and dry creek beds. Bat species, mass, and sex were recorded for all captures. I assessed age (juvenile or adult) based on the degree of ossification of the metacarpal-phalanx joints (Racey 1974) and female reproductive condition by abdominal palpation and by inspecting the mammae (Kunz

1988). I followed the guidelines of the American Society of Mammalogists for the capture, handling, and care of mammals (Animal Care and Use Committee 1998).

I used radio transmitters (Blackburn Transmitters, Nacogdoches, Texas, USA and Holohill Systems Limited, Ontario, Canada) to locate bats at their diurnal roost sites from mid-May to early August. Transmitters were bonded to the mid-scapular region with Skin-Bond® surgical adhesive following partial hair removal. Depending on the species of bat, individuals were instrumented with 0.24−0.71-g transmitters with 11−21-day batteries. Transmitter load was generally <5% of body mass (Aldridge and Brigham 1988).

I tracked each bat to its roost site in the morning following capture and about five days/week until its signal was lost. I used five 15.3-m radiotelemetry towers (each equipped with 2 2-m, 13-element, high-gain yagi antennas), situated on the highest elevations in the basin, to determine general bat locations and hand-held yagi antennas to locate exact roost locations (trees or snags). To ensure that locations were as accurate as possible, bats were visually located either from the ground using binoculars and spotting scopes or by climbing the tree. Because individual tree bats often roost in multiple roost sites (e.g., Menzel et al. 1998), instrumented bats were relocated as often as possible; thus, I located multiple roosts for most individual bats. I collected Global Positioning System (GPS) coordinates for each bat location using Rockwell® PLGR GPS receivers (Rockwell-Collins, Cedar Rapids, Iowa, USA). Based on field observations, these units typically had an accuracy of ±10 m.

Vegetation mapping

Spatial analyses were conducted using both ArcMap® 3.2 and ArcView® 9.0 (Environmental Systems Research Institute, Redlands, California, USA). Vector maps of forest stand boundaries were obtained from ONF. Because those maps were digitized from topographic maps in which stand boundaries were hand-drawn, they were relatively inaccurate. Therefore, to more accurately reflect the size and shape of forest stands, stand boundaries were redrawn using a 10-m digital color orthoquad (DOQ) as a template. Forest stands were classified based on the Continuous Inventory and Stand Condition Management System (CISC) database maintained by the Fourche-Jessieville-Winona Ranger District of ONF. To ensure vegetation maps were accurate, forest types and conditions such as age and past silvicultural treatments were ground-checked and corrected in the data layer. Tree core data from most stands were used to verify stand ages. Boundaries for habitat classes on industrial timberlands were digitized from 10-m DOQs and classified by ground-truthing.

I classified each stand into 1 of 13 forest habitat classes (Table 2.1). For mostly even-aged stands, habitat classifications were based on age and forest type (pine or hardwood). Stands not subjected to even-aged management were classified based on silvicultural system. I differentiated hardwood and pine stands because some species of bats (e.g, Seminole bats, *L. seminolus*) roost primarily in pines, whereas others (e.g., eastern red bats) roost primarily in hardwoods (Menzel et al. 1998). I differentiated even-aged stands by age because age (along with past management) was a primary determinant of vertical structure and tree density (both indices of structural clutter) within forest stands (e.g., Baker et al. 1996). All age classes were based on ages of stands in the year

2000. I chose age classes based on stand successional stages presented by Baker et al. (1996) for pine types in the southeastern U.S. I derived the following age classes for primarily even-aged stands based on personal observations of relationships between successional stage and age: stands <15 years old (stand initiation phase); stands 15−29 years old (early stem exclusion phase); stands 30−49 years old (late stem exclusion stage); stands 50−100 years old (understory reinitiation stage); and stands over 100 years old (old growth stage). To reduce number of classes included in the analysis, habitats that were uncommon in the basin were removed from analyses; those habitats included young clearcuts and hardwood stands 30−49 years old. Stands of like type were combined and a 5-m raster grid was created for analyses.

I used broad categories for forest type to reduce "fuzzy" edges that existed between adjacent stands that differed only slightly in pine or hardwood composition. Older pine stands typically contained a hardwood component; thus, predominantly pine, pine-hardwood, and hardwood-pine stands were designated as mixed pine-hardwood for mature classes (>50 years old). Pure hardwood forest types were designated simply as hardwood stands; this included most SMZs. Because of historical management in the basin, most even-aged stands <30 years old were pine with a limited hardwood component.

Silviculture treatments that resulted in similarly structured conditions were combined. Thus, single-tree selection stands and pine-woodland restoration areas, which were initially treated with similar thinning, midstory removal, and burning in 2000, were grouped into a "thinned mature" class. Private industrial timberlands in the basin were managed using intensive even-aged management. Most of those lands were short-

rotation, loblolly-pine plantations with little hardwood component. Thus, I used three habitat classes for industrial plantations: young open clearcuts (about <10 years old), closed-canopy plantations (about 10−18 years old), and older thinned plantations (about ≥19 years old).

Topographic features

I included elevation, slope, and distance to streams and roads in analyses as topographic features. No paved roads existed within the basin; primary roads were gravel and not frequently traveled. I included both primary gravel roads and secondary roads, which included gated roads, recently-closed roads, and four-wheel drive trails. Data layers containing locations of roads and streams, which were originally digitized from topographic maps, were obtained from ONF. Stream and road locations were corrected using DOQs to more accurately reflect road and stream locations. I collected locations of secondary roads either by digitizing from the DOQ or by GPS. Stream data layers included wildlife ponds (ponds < 0.5 ha created in upland areas as a water source for wildlife), although those were uncommon in the basin. I used a 10-m digital elevation model (DEM) of the study area to determine elevation and slope at each roost location.

Random locations

To determine if attributes of the landscape differed between roost locations and random sites, I created a set of random locations for each species of bat. A primary concern in studies of resource selection is the designation of study-area boundaries because resource availability is defined as the quantity of resources accessible to the

animal, not the quantity available in the environment (Alldredge et al. 1998). Determining boundaries of "available" habitat is critical to the results of any resource selection study (Aebischer et al. 1993). Therefore, to determine the area of available habitats where random locations were generated, I created a concave polygon that encompassed the outer-most roosts in the study area. I then created a 100-m buffer around the exterior of this polygon; I considered that polygon (including the buffered area) the area of habitat available to bats. I created separate availability polygons for each species of bat. All random locations were generated within this polygon, but distances from roosts and random points to the nearest road or stream included roads and streams that fell outside this polygon. I generated two random points for each individual bat within the area of available habitat for that species using a random location generator (Hawth's tools; http://www.spatialecology.com).

Data analysis

Landscape theorists suggest that landscape structure and function possesses an inherent scale at which identifiable processes occur (Carlile et al. 1989, Turner 1989, Turner et al. 1989). However, theoretical or empirical reasons for selecting the extent at which I evaluated landscape-level relationships were limited; therefore, I modeled these relationships at 2 spatial extents to determine if relationships between locations of roosts and landscape metrics were resilient to changes in scale. I characterized patch configuration and habitat abundance of the landscape in 250-m and 1,000-m radii surrounding each random and roost location. I considered the 1,000-m radius area similar in scale to home-range selection within the study area. Although limited

information is available on home-range size of many forest bats in the southeastern U.S, the 1,000-m radius corresponded roughly with the average maximum distance traveled by red bats during foraging in forested environments of the Southeast (Elmore et al. 2005) and the average distance (1,137 m) between roost locations and foraging areas for eastern pipistrelles (Krishon et al. 1997). I used the 250-m radius to provide insight on more site-specific locations of roosts. At each roost and random location, the two regions (19.6 ha and 314.2 ha) were clipped from vegetation maps. Landscape patch metrics (Table 2.2) along with total area in each forest habitat class (Table 2.1) were then calculated for each of the two extents using Patch Analyst Grid (McGarigal and Marks 1995, Elkie et al. 1999).

For each species (and the bat community as a whole), I created two logistic regression models (small- and large-extent) to determine the best set of factors among forest habitat classes, patch configuration, and topographic metrics that predicted occurrence of roosts. Model selection was in four steps. First, because independent variables used in regression techniques are limited by number of observations (Pedhazur 1997), I reduced total numbers of variables included in analyses. To reduce multicollinearity, patch metrics that were highly correlated ($r \geq 0.70$) with ≥ 4 other variables at the 1,000-m extent, or ≥ 7 variables at the 250-m extent were removed, leaving 8 patch metrics (Table 2.2). Second, I used stepwise logistic regression (PROC LOGISTIC; SAS Institute Inc. 2000) to select remaining variables to include in candidate models for each species of bat at each of the two extents. Third, to determine the set of candidate models for each species of bat and extent, I used a best subsets procedure, which selected the best 1-variable model, best 2-variable model, and so forth based on

values of the chi-square statistic (SAS Institute Inc. 2000). Finally, I determined the most parsimonious model among all candidate models based on the lowest value of Akaike's Information Criteria (AIC; Burnham and Anderson 2002). I used the modified criterion (AIC_c) for small samples for all comparisons (Anderson et al. 2000).

To reduce the likelihood of overfitting models, the maximum number of independent variables allowed in candidate models was constrained such that a minimum of 10 observations had to be present for each independent variable included in the model (Peduzzi et al. 1996). To reduce the influence of independent variables with imprecise or erroneous estimates, I removed candidate models that contained variables with unusually large standard errors (e.g., Gutzwiller and Barrow 2001) and removed variables from models that caused complete or quasi-complete separation of data (Hosmer and Lemeshow 2000). I evaluated overall model fit using a generalized maximum-rescaled R^2 (Nagelkerke 1991) and percent concordance (Hosmer and Lemeshow 2000, SAS Institute Inc. 2000).

Because individuals frequently roosted at different sites within the same general area over multiple days, roost locations for individuals were not independent (Hurlbert 1984). To eliminate spatial autocorrelation, I considered the individual bat as the experimental unit (Miller et al. 2003) by averaging all landscape metrics for each individual. Although differences may have occurred in site selection between sexes of the same species, sample size was not large enough for most species for analysis by sex. Further, regression techniques are large-sample techniques, and model accuracy is dependent on the number of samples (Pedhazur 1997). Therefore, I combined sexes so that, in most cases, models represented habitat relationships for the species as a whole.

For evening bats (*Nycticeius humeralis*) and Seminole bats, only males were included in the models because adult females of those two species were not captured in the basin. The majority of individuals were adults. Juveniles made up 7% of red bats, 14% of northern longear myotis (*Myotis septentrionalis*), and 14% of eastern pipistrelle bats. All evening bats, Seminole bats, and big brown bats (*Eptesicus fuscus*) were adults.

To model selection of roosts by the entire bat community, I combined all species to create small- and large-extent models. Because red bats and northern longear myotis made up 52% of individuals in the data, using all individuals of all species would have weighted community-level results heavily toward these two species. Therefore, I randomly selected 16 adult individuals of each species so that all species were weighted equally in the analyses. For each species, equal numbers of each sex were included when possible. For the bat community data set, I created a separate polygon for the area of available habitat and used metrics from a set of random points generated within this polygon.

Elevation, slope, and distance to nearest road or stream were not scale-dependent; thus, those measurements were included in both scale-dependent models. To determine if locations of bat roosts differed from random placement in relation to roads and streams, I calculated the minimum Euclidean distance from each roost and random location to the nearest road and stream by creating a 5-m raster grid for distance to roads and streams. Roost and random locations were overlaid on those two distance grids, and distance values were output for analyses.

RESULTS

From 2000−2005, I captured 715 bats during 344 net nights. I located 426 roosts from 162 individuals of 6 species (Table 2.3). An additional 12 roosts of 9 hoary bats (*Lasiurus cinerius*) were not included in analyses because samples were too few for multiple logistic regression. I captured no adult female Seminole or evening bats in the basin during the period of summer under study. Two juvenile female evening bats were captured and tracked to roosts in late July but were not included in analyses. Those two individuals were likely dispersing from other areas because I lacked evidence to suggest that female evening bats were present or reproducing in the basin. I captured three female Seminole bats in mid-September. Female Seminole bats have been collected elsewhere in Arkansas but all were captured in late summer (August−September; Wilhide et al. 1998).

Big brown bats

At the 250-m extent, the logistic model relating landscape attributes to presence of roosts for big brown bats had an AIC_c of 53.92, concordance of 85.2%, and a maximum- rescaled R^2 of 0.44. At the 1000-m extent, AIC_c was 58.40, concordance was 80.5%, and maximum-rescaled R^2 was 0.34. At both extents, this species was associated with areas of the basin with less slope, higher elevation, and closer to streams than random locations (Table 2.4). At the 250-m extent, roosts were associated with areas containing abundant group selection harvests. At the 1,000-m extent, big brown bats selected areas of the basin with greater amounts of old-growth hardwoods (≥100 years

old). This species was more likely to roost in upland areas of the basin that were dominated by unharvested or partially-harvested mature stands.

Northern longear myotis

At the 250-m extent, the logistic model relating landscape attributes to presence of roosts for northern longear myotis had an AIC_c of 142.74, concordance of 77.5% and a maximum- rescaled R^2 of 0.28. At the 1000-m extent, AIC_c was 135.180, concordance was 81.9%, and maximum-rescaled R^2 was 0.38. At the 250-m extent, this species was more likely to roost in areas with abundant thinned mature forest and lower amounts of young pine stands 15 −29 years old (Table 2.4). Furthermore, their roosts were closer to roads than random locations. At the 1,000-m extent, roosts were more likely to be in areas that had pine seed-tree stands, and low amounts of closed canopy and thinned loblolly pine plantations (industrial timberlands). At the large extent, this species was associated with lower amounts of mixed pine-hardwood stands 50−99 years old, but greater amounts of this forest type ≥100 years old. At both extents, this species was more likely to roost in areas of the basin with greater slope. In general, this species roosted in upland areas of the basin that were steep, dominated by unharvested or partially harvested stands, and did not contain industrial timberlands.

Evening bats

At the 250-m extent, the logistic model relating landscape attributes to presence of roosts for male evening bats had an AIC_c of 49.485, concordance of 91.3%, and a maximum-rescaled R^2 of 0.60. At the 1000-m extent, AIC_c was 58.84, concordance was

77.3%, and maximum-rescaled R^2 was 0.30. At the 250-m extent, this species was associated with areas of abundant mature trees; roost locations for evening bat males had greater amounts of group selection harvesting, thinned mature forest, and hardwood and mixed pine-hardwood stands 50−99 years old than random locations (Table 2.4). Further, roost locations were more likely to have a lower MPS. At the 1,000-m extent, evening bats roosted in regions of the basin with more thinned mature forest and hardwood forests 50−99 years old than random locations.

Eastern red bats

At the 250-m extent, the logistic model relating landscape attributes to presence of roosts for eastern red bats had an AIC_c of 154.60, concordance of 72.7%, and a maximum-rescaled R^2 of 0.19. At the 1000-m extent, AIC_c was 160.42, concordance was 62.6%, and maximum-rescaled R^2 was 0.09. At the 250-m extent, this species roosted in areas with greater amounts of group selection and old-growth mixed pine-hardwood forest than random locations (Table 2.4). Furthermore, roosts were associated with lower MSI, indicating they were more likely to roost in areas where forest patches were blocky in shape. At both extents, locations of red bats roosts had a greater LPI than random locations, indicating areas of the basin where roosts were located were more likely to be dominated by large blocks of similar forest. For both models, roosts were located closer to roads than random locations. At the 1,000-m extent, roosts were more likely to be in areas that contained seed-tree stands than random.

Seminole bats

At the 250-m extent, the logistic model relating landscape attributes to presence of roosts for male Seminole bats had an AIC_c of 46.23, concordance of 91.2%, and a maximum-rescaled R^2 of 0.61. At the 1000-m extent, AIC_c was 43.73, concordance was 93.6%, and maximum-rescaled R^2 was 0.68. At the 250-m extent, roosts of this species were located in areas with greater amounts of group selection, thinned mature, and thinned loblolly pine plantations than random locations, indicating this species was associated with open forest stands that contained abundant mature pines (Table 2.4). At the 1,000-m extent, roosts of Seminole bats were more likely to be located in regions of the basin that had greater amounts of group selection and thinned mature forest and lower amounts of mixed pine-hardwood forest 30−49 years old. Their roost locations were in areas with lower amounts of closed canopy loblolly pine plantations than random locations. At both scales, roosts were located closer to streams than random locations.

Eastern pipistrelles

At the 250-m extent, the logistic model relating landscape attributes to presence of roosts for eastern pipistrelles had an AIC_c of 88.63, concordance of 84.3%, and a maximum-rescaled R^2 of 0.46. At the 1000-m extent, AIC_c was 93.18, concordance was 81.6%, and maximum-rescaled R^2 was 0.35. At the 250-m extent, this species was more likely to roost in areas with more group selection, thinned mature forest, hardwood forest 50−99 years old, and old growth mixed pine-hardwood forest, indicating this species was more likely to be found in upland areas that contained mature hardwoods (Table 2.4). At the 1,000-m extent, roosts were located in areas of the basin with lower amounts of

mixed pine-hardwood forest 50−99 years old and greater LPI than random locations, indicating this species was associated with areas dominated by large patches of similar forest. Patch richness had a positive effect at the small extent but a negative effect at the large extent. At the both scales, roosts were located farther from roads than random.

All species

At the 250-m extent, the logistic model relating landscape attributes to presence of roosts for the bat community had an AIC_c of 315.91, concordance of 78.4%, and a maximum- rescaled R^2 of 0.31. At the 1000-m extent, AIC_c was 344.91, concordance was 68.2%, and maximum-rescaled R^2 was 0.15. At the 250-m extent, roosts for the bat community as a whole were associated with recent partially harvested or unharvested stands that contained mature trees (Table 2.4). Locations of roosts also were in areas with lower MPS and lower patch richness. At the 1,000-m extent, roosts were more likely to be located in areas of the basin with low amounts of closed-canopy loblolly pine plantations. At the large extent, roosts were located in areas of the basin with less mixed pine-hardwood forest 50−99 years of age, whereas at the 250-m scale, roost locations contained more of this habitat class. At both scales, bats tended to roost in closer proximity to streams than random locations and were less likely to roost in areas with abundant pine stands <15 years old than random locations. The bat community generally roosted away from areas dominated by dense or young stands of pine.

DISCUSSION

Scale

In general, forest cover and management patterns differed throughout the basin according to slope, aspect, soils, and ownership; these fundamentally different regions were aggregated in large blocks relative to typical stand sizes (usually 16−18 ha). Most lowland areas were intensively managed by Weyerhaeuser. Regions of the basin with moderate slope and south-facing aspects were primarily natural pine forests and were managed by USFS for timber production; these areas included substantial amounts of partial harvesting. North slope areas were dominated by hardwoods and areas in the basin too steep (generally >35%) for logging operation were typically mature or old-growth forest with little silvicultural activity. Thus, the larger extent analysis (1,000-m) generally characterized roost selection among these broad categories of management, whereas the small extent (250-m) was more indicative of selection among forest habitat classes by bats within these broader areas of management.

Maximum-rescaled R^2 and concordance values suggested that small-extent models were a better fit in 4 of 6 species than large-extent models. Values of maximum-rescaled R^2 averaged 0.40 for all small-extent models and 0.33 for all large-extent models. For all species combined, R^2-values were relatively low (0.15) for the large-extent model but substantially higher for the small-extent model (0.31). Models for most species had relatively high R^2-values, with the exception of the models for red bats (250-m extent = 0.19, 1,000-m extent = 0.09). Unlike this study, Gorrensen et al. (2005) found a greater number of significant responses in abundance of bat species to landscape patch metrics at larger than smaller scales. Among all models, the average number of patch

configuration metrics included in large-extent models was 0.43, and the average number of patch metrics included in small-extent models was 1.0.

Forest habitat classes

Consistent with prediction 3, for most species, forest habitat classes were included more often than patch configuration or topography in models differentiating roost from random locations. Amount of a particular habitat made up an average of 60% of the metrics included in small-extent models and an average of 63% of metrics included in large-extent models. Studies on bat activity suggest that microhabitat effects are typically stronger than landscape-level effects (Krusic et al. 1996, Zimmerman and Glanz 2000, Gehrt and Chelsvig 2003), and I created forest habitat classes based on differences in forest structure that would potentially affect microhabitat. Thus, it is not surprising that habitat classes had a strong influence on roost locations.

Consistent with prediction 1, 4 of 6 species models at the small extent demonstrated a positive association with recently thinned mature forest and 5 of 6 species models demonstrated a positive association with recently harvested group selection areas. At the large extent, 2 of 6 species were associated with recently thinned mature forest, and only one species was associated with group-selection areas. For the bat community as a whole, both habitat classes were important at the small extent but not the large extent. Most species were more likely to roost in areas within or in close proximity to areas of recent partial harvesting or thinned forest that retained a component of mature overstory trees. This finding is consistent with prediction 1 and is consistent with previous work on the effects of bats and clutter. Studies suggest many bat species prefer

roosting in stands with low tree density (e.g., Hutchinson and Lacki 2000, Menzel et al. 2001) and low canopy coverage (e.g., Sasse 1995, Vonhof and Barclay 1996, Brigham et al. 1997a). Thus, stands with reduced structure, derived naturally or silviculturally, may prevail over other aspects of the landscape in affecting selection of roosting habitat by forest bats.

The majority (about 95%) of partially harvested areas in the basin were recently cut. Over longer periods, uneven-aged stands, including those harvested via single-tree selection and group selection, will become more cluttered as regeneration occurs and additional cohorts of trees are added to the stand structures. Although these harvest methods initially created open stands with little midstory, they will likely become more cluttered than mature even-aged stands.

Topographic metrics

Topographic metrics were included in the models more often than patch configuration metrics. At the small extent, an average of 60% of non-habitat class variables included in models were topographic variables; an average of 81% of non-habitat class variables included in models were topographic variables at the large extent. Consistent with prediction 2, distance to streams was included in 2 of 6 small-extent species models, 2 of 6 large-extent species models, and both models for all species combined. Kalcounis-Ruppell et al. (2005), in a meta-analysis of published studies of bat roosting, found a general trend of roosts being located closer to water than random placement.

Distance to roads was included in 3 of 6 small-extent species models and 2 of 6 large-extent species models. Roads act as corridors, filters, edges, and barriers in landscapes (Forman 2003). Areas near roads may have a higher abundance of predators, and thus higher rates of predation compared with other locations. For example, two of the most common predators of birds and bird nests in the Ouachita Mountains, the raccoon (*Procyon lotor*) and the black rat snake (*Elaphe obsoleta obsoleta*), favor hard forest edges for hunting (Durner and Gates 1993, Pedlar et al. 1997). Thus, bats might be expected to avoid roosting near roads if predation pressures were greater in these areas. However, many studies have failed to demonstrate increased nest predation on birds nesting in proximity to roads (e.g., Yanner and Mahan 1997, Lindenmayer et al. 1999, Ortega and Capen 2002, King and DeGraaf 2002). In contrast, studies suggest that roads provide flight corridors or navigational references for bats (Limpens and Kapteyn 1991, Walsh and Harris 1996, Grindal and Brigham 1998), and some bat species tend to forage and commute in edge habitats over forest interiors and open non-forested areas (Ekman and de Jong 1996, Grindal and Brigman 1999, Verboom and Spoelstra 1999, Hogberg et al. 2002). Consequently, some bat species might roost in close proximity to travel corridors.

Contrary to prediction 2, for 3 of 6 species and the bat community as a whole, roads appeared to have little effect on roost placement, perhaps because so much of the area had been recently thinned. Prior to thinning, roads would have offered the least cluttered travel corridors for bats. Roosts of eastern red bats were more likely to be closer to roads than random locations at both scales, which was consistent with prediction 2. However, roosts of eastern pipistrelles were more likely to be further from roads than

random locations at both scales, which was contrary to prediction 2. Consequently, there may be trade-offs between selecting areas close to travel corridors and potentially increased predation resulting from roosting closer to potential predator corridors, and these life-history traits may differ among species. However, the eastern pipistrelle is considered a clutter-adapted species (Menzel et al. 2005) and may utilize roads less than other species.

Patch configuration metrics

Among the patch configuration metrics, largest patch index (LPI) was important in large-extent species models for eastern pipistrelles and both models for eastern red bats (both vegetation-roosting bats), suggesting that these two species favored areas dominated by large blocks of similar forest. Patch richness was included in large- and small-extent models for eastern pipistrelles; however at the small extent, this species was associated with areas containing more habitat types whereas at the large extent they favored areas with fewer habitat types (more homogeneous forest). Eastern pipistrelles likely selected diverse sites for roosting but generally roosted in regions of the basin dominated by certain management methods such as partial harvesting.

Availability of roosting structure

The big brown bat, northern longear myotis, and evening bat are cavity and crevice-roosting species, and most of their roosts were located under exfoliating bark or in the crevices of snags. All big brown roosts were located in pine snags, whereas 58% of male evening bat roosts and 89% of northern longear myotis roosts were in pine or

hardwood snags. I generated random locations geographically and without regard to available structure such as snags. Random locations could have been unusable by these species if snags did not occur at random sites. However, a wide-spread ice storm in winter 2000−2001 created abundant snags throughout the basin. Consequently, few locations within the basin were limited in numbers of snags, and it is unlikely that snags were unavailable at most random locations. Nonetheless, it is unknown if or to what extent snag abundances varied geographically throughout the basin. Higher elevations are prone to more frequent ice accumulations and may have differed in snag abundance from lowland areas, and trees located in thinned or partially harvested areas tend to succumb to mortality from wind damage, lightening, and ice accumulation more than trees located in denser stand conditions. Regardless, vegetation-roosting species (eastern red, Seminole, and eastern pipistrelle) that are not associated with snags also selected these partially-harvested or thinned areas, indicating that the structure of the stand, not abundance of snags, was the principle factor making these areas favorable roosting sites for most species.

Vegetation-roosting species would be less influenced by available structure at random locations than snag-obligate species because these species select relatively abundant structures such as mature live trees. Eastern red bats roosted almost exclusively in deciduous hardwoods, Seminole bats roosted exclusively in pines, and eastern pipistrelles roosted primarily in the dead leaves of deciduous trees. Thus, roost structure was not limited throughout the basin for red and eastern pipistrelle bats (with the possible exception of some industrial pine plantations that lacked hardwoods), and Seminole bats were limited to areas that contained pines.

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Table 2.1. Forest habitat classes included in logistic regression models of landscape-level roost selection by forest bats in the Ouachita Mountains of west-central Arkansas, 2000−2005.

Habitat class	Description[a]
Pine <15 yrs	Even-aged pines, <15 years old
Pine 15−29 yrs	Even aged pines, 15−29 years old
Pine 30−49 yrs	Even-aged pines, 30−49 years old
Hardwood 50−99 yrs	Hardwood stands, primarily even-aged, 50−99 year old
Hardwood ≥ 100 yrs	Hardwood stands ≥100 years old
Mixed P/H 30−49 yrs	Mixed pine and hardwood stands, primarily even-aged, 30−49 years old
Mixed P/H 50−99 yrs	Mixed pine and hardwood stands, primarily even-aged, 50−99 years old
Mixed P/H ≥ 100 yrs	Mixed pine and hardwood stands, ≥100 years old
Group selection	Mature mixed pine-hardwood stands that had undergone mostly recent group selection harvest and matrix thinning
Thinned mature	Mature (> 50 years old) mixed pine-hardwood stands that had undergone recent partial overstory reduction and midstory removal; included young single-tree selection stands and pine woodland restoration areas
Pine seed-tree	Seed-tree cuts, open stands with scattered mature pines left for seed production
Industrial timberlands	
Closed plantation	Closed-canopy loblolly pine plantations, approximately 14−25 years of age
Thinned plantation	Older/thinned loblolly pine plantations, approximately 20−35 years of age

Table 2.1. –continued.

[a]See study area description for more detail on silviculture treatments.

Table 2.2. Topographic and patch configuration metrics included in logistic regression models of landscape-level roost selection by forest bats in the Ouachita Mountains of west-central Arkansas, 2000−2005.

Landscape metric	Description
Number of patches	Total number of patches in a designated landscape area (number)
MPS[a]	Mean patch size in the landscape region (ha)
PSCOV[a]	Patch size coefficient of variation = patch size standard deviation/mean patch size (%)
MSI[a]	Mean shape index (average perimeter to area ratio); range ≥ 1; equals 1 when all patches are circular (square for raster data sets)
IJI[a]	Interspersion juxtaposition index; measurement of patch adjacency; range from 0 (uneven distribution) to 100 (all patches are equally adjacent; %)
SEI[a]	Shannon's evenness index for patch types
LPI[a]	Largest patch index; percentage of landscape comprised of the largest patch (%)
Patch richness	Number of patch types present (number)
Elevation	Elevation from digital elevation model (m above mean sea level)
Slope	Slope from digital elevation model (%)
Distance to streams	Euclidean distance to nearest stream (m)
Distance to roads	Euclidean distance to nearest road (m)

[a] Complete mathematical description of metric in McGarigal and Marks (1995).

Table 2.3. Numbers of individual bats (by sex) and numbers of diurnal summer roosts for six species of bat included in logistic regression models of landscape-level roost selection in the Ouachita Mountains of west-central Arkansas, 2000−2005.

Species	No. of individuals		No. of roosts per individual		Total no. of roosts
	Male	Female	Range	Mean	
Big brown	12	4	1−5	2.1	34
Northern longear myotis	21	21	1−7	2.4	102
Evening bats	17	0	1−8	2.5	45
Eastern red bat	22	20	1−9	3.5	145
Seminole Bat	17	0	1−6	3.0	51
Eastern pipistrelle	21	7	1−5	1.8	49
Total	110	52	1−9	2.8	426

Table 2.4. Logistic regression models for landscape-level selection at 2 spatial extents surrounding diurnal summer roosts of 6 bat species, and all species combined in a diverse forest landscape of the Ouachita Mountains of west-central Arkansas, 2000−2005.

	Spatial extent					
	250-m			1,000-m		
Bat species and Variable	Estimate	$P > \chi^2$	Odds[a]	Estimate	$P > \chi^2$	Odds[a]
Big brown bat						
Intercept	-18.619	0.009		-12.540	0.030	
Group selection	0.276	0.020	1.318			
Hardwoods ≥ 100 yrs				0.229	0.193	1.258
Elevation	0.057	0.007	1.059	0.041	0.019	1.042
Slope	-0.122	0.051	0.885	-0.153	0.024	0.858
Distance to streams	-0.007	0.111	0.993	-0.005	0.153	0.995
Northern longear myotis						
Intercept	-1.387	0.020		-0.040	0.953	
Pine 15−29 yrs	-0.198	0.247	0.821			
Closed plantation				-0.019	0.064	0.981
Thinned plantation				-0.017	0.110	0.983
Mixed P/H ≥ 100 yrs				0.029	0.004	1.030
Mixed P/H 50−99 yrs				-0.026	0.000	0.975
Seed-tree				0.058	0.039	1.060
Thinned mature	0.064	0.013	1.066			
Slope	0.072	0.012	1.075	0.051	0.103	1.052
Distance to roads	-0.005	0.007	0.995			
Evening bat						
Intercept	-11.277	0.035		-2.266	0.001	
Group selection	0.878	0.024	2.407			

Table 2.4. –continued.

Bat species and Variable	Spatial extent					
	250-m			1,000-m		
	Estimate	$P > \chi^2$	Odds[a]	Estimate	$P > \chi^2$	Odds[a]
Thinned mature	0.773	0.021	2.166	0.007	0.071	1.007
Hardwoods 50−99 yrs	1.908	0.026	6.741	0.048	0.006	1.049
Mixed P/H 50−99 yrs	0.635	0.040	1.887			
MPS	-0.247	0.052	0.781			
Eastern red						
Intercept	0.681	0.750		-1.103	0.040	
Group selection	0.092	0.016	1.096			
Mixed P/H ≥ 100 yrs	0.240	0.052	1.271			
Seed-tree				-0.071	0.189	0.932
MSI	-1.782	0.130	0.168			
LPI	0.018	0.082	1.019	0.020	0.060	1.020
Distance to roads	-0.004	0.056	0.996	-0.003	0.080	0.997
Seminole						
Intercept	-1.594	0.104		-0.691	0.472	
Group selection	0.223	0.019	1.250	0.035	0.058	1.036
Thinned mature	0.280	0.000	1.323	0.029	0.001	1.029
Mixed P/H 30−49 yrs				-0.074	0.085	0.929
Thinned plantations	0.200	0.048	1.221			
Closed plantation				-0.145	0.155	0.865
Distance to streams	-0.001	0.025	0.990	-0.011	0.031	0.989
Eastern pipistrelle						
Intercept	-7.724	0.000		2.419	0.155	
Group selection	0.318	0.000	1.375			

Table 2.4. –continued.

Bat species and Variable	Spatial extent					
	250-m			1,000-m		
	Estimate	$P > \chi^2$	Odds[a]	Estimate	$P > \chi^2$	Odds[a]
Thinned mature	0.269	0.001	1.309			
Hardwoods 50−99 yrs	0.270	0.002	1.310			
Mixed P/H 50−99 yrs				-0.018	0.011	0.982
Mixed P/H ≥ 100 yrs	0.423	0.000	1.526			
Patch richness	0.831	0.038	2.295	-0.655	0.003	0.517
LPI				0.042	0.020	1.042
Distance to roads	0.005	0.065	1.005	0.003	0.102	1.004
All Species						
Intercept	-1.837	0.260		-0.758	0.023	
Closed plantation				-0.011	0.031	0.989
Pine < 15 yrs	-1.595	0.363	0.203	-0.035	0.017	0.966
Hardwoods 50−99 yrs	0.274	0.000	1.315			
Mixed P/H 50−99 yrs	0.161	0.002	1.175	-0.012	0.000	0.988
Mixed P/H ≥100 yrs	0.262	0.000	1.300			
Group selection	0.234	0.000	1.264			
Thinned mature	0.255	0.000	1.290			
Thinned plantation	0.192	0.002	1.213			
Distance to streams	-0.003	0.029	0.997	-0.002	0.129	0.998
MPS	-0.136	0.021	0.873			
Patch richness	-0.408	0.208	0.665			

[a] Comparison of roost sites with random locations: odds = odds ratio of roost site/random site.

VITA

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Candidate for the Degree of

Doctor of Philosophy

Dissertation: STAND- AND LANDSCAPE-LEVEL ROOST SELECTION BY FOREST BATS IN THE OUACHITA MOUNTAINS

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Title of Study: STAND- AND LANDSCAPE-LEVEL ROOST SELECTION BY FOREST BATS IN THE OUACHITA MOUNTAINS

Pages in Study: 87 Candidate for the degree of Doctor of Philosophy

Major Field: Wildlife and Fisheries Ecology

Scope and Method of Study: The purpose of this study was to determine roosting habitat preferences by forest bats and to create landscape-level models to determine characteristics of the landscape that were associated with roosting locations. I located 428 roosts from 162 individual bats of 6 species. Using Euclidean distance statistics and the individual bat as the experimental unit, I determined preference and avoidance for 13 habitat types in the Ouachita Mountains of central Arkansas. I also used logistic regression to create scale-dependent models that differentiated habitat classes, topography, and landscape patch metrics of roost locations from random locations.

Findings and Conclusions: In general, most bat species preferred to roost in stands that had been partially harvested and contained few midstory trees. The most preferred habitats were partially harvested mixed pine-hardwood stands and stands ≥99 years old. Although highly available, second-growth mixed pine-hardwood stands that were 50−99 years old were only preferred by 1 bat species. Forest habitat classes were included more often that topographic or patch-configuration metrics in landscape models. Fine-scale models were a better fit than broad-scale models for most species. Most models included habitat classes of partially harvested or thinned forest that retained mature overstory trees. For all species combined, bats were more likely to roost in close proximity to water sources and in areas that contained less dense or young forest than random locations.

Advisor's Approval: David M. Leslie, Jr.