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# Scale-Dependent Effects of Landscape Structure and Composition on Diurnal Roost Selection by Forest Bats

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**ABSTRACT** Forest management affects the quality and availability of roost sites for forest-dwelling bats, but information on roost selection beyond the scale of individual forest stands is limited. We evaluated effects of topography (elevation, slope, and proximity of roads and streams), forest habitat class, and landscape patch configuration on selection of summer diurnal roosts by 6 species of forest-dwelling bats in a diverse forested landscape of the Ouachita Mountains, Arkansas, USA. Our objectives were to identify landscape attributes that potentially affect roost placement, determine whether commonalities exist among species in their response to landscape attributes, and evaluate the effects of scale. We modeled roost selection at 2 spatial scales (250- and 1,000-m radius around each roost). For each species, parameters included in models differed between the 2 scales, and there were no shared parameters for 2 species. Average coefficients of determination ($R^2$) for small-scale models were generally higher than for large-scale models. Abundance of certain forest habitat classes were included more often than patch configuration or topography in differentiating roost from random locations, regardless of scale, and most species were more likely to roost in areas containing abundant thinned forest. Among topographic metrics, big brown bats (*Eptesicus fuscus*) were more likely to roost at higher elevations; roosts of big brown bats, northern long-eared bats (*Myotis septentrionalis*), and Seminole bats (*Lasiurus seminolus*) were influenced by slope; and big brown bats, evening bats (*Nycticeius humeralis*), and Seminole bats were more likely to roost closer to water than random. Northern long-eared bats and red bats (*Lasiurus borealis*) were more likely to roost closer to roads, whereas eastern pipistrelles (*Perimyotis subflavus*) were more likely to roost further from roads than random. Common parameters in most models included 1) positive associations with group selection (5 of 6 species) and thinned mature forest (4 species) at the small scale; 2) negative associations with unmanaged mixed pine–hardwood forest 50–99 years old at the large scale (4 species); 3) negative association with stands of immature pine 15–29 years old at the small scale (3 species); and 4) a positive association with largest patch index at the large scale (3 species). Our results suggest that, in a completely forested landscape, a variety of stand types, seral stages, and management conditions, varying in size and topographic location throughout the landscape, would likely provide the landscape components for roosting required to maintain a diverse community of forest bats in the Ouachita Mountains. (JOURNAL OF WILDLIFE MANAGEMENT 72(4):913–925; 2008)

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Little is known about the relationships between bat roosting and landscape structure, partly because most studies relating bat roosting to forest structure generally have been performed at scales at or below the forest stand. At the forest-stand scale, studies suggest that forest management can be used to provide favorable roosting sites for various forest-dwelling bats (e.g., Crampton and Barclay 1998, Rabe et al. 1998, Perry et al. 2007). By manipulating forest-stand age, tree density, understory and midstory condition, and by creating snags, land managers can theoretically provide more favorable roosting sites for bats within individual stands in forests. However, if attributes of the surrounding landscape are as important as forest-stand characteristics, land managers need to know how landscape attributes and stand management interact to affect roost selection by forest bats.

Landscape attributes such as topography, proximity to water sources or roads, edge, and patch configuration could alter fitness of roosting bats by affecting predation rates, flight distances and energy expenditure, frequency of disturbance, and microclimate. Thus, landscape attributes could potentially affect where bats roost. For example, roosts are often located closer to water sources than random (Kalcounis-Rüppell et al. 2005), likely because of high insect abundance and water needs, and topographic attributes such as slope or elevation may affect roost location for some species, likely because of microclimate differences associated with topography (e.g., Ormsbee and McComb 1998, Rabe et al. 1998, Baker and Lacki 2006). Recently, researchers have began to study effects of patch arrangement and topographic features on activity and relative abundance of bats via mist nets and acoustic detectors (e.g., Gehrt and Chelsvig 2003, Gorrensen and Willig 2004, Ford et al. 2006, Loeb and O'Keefe 2006), but studies examining effects of landscape attributes on roost selection (e.g., Rabe et al. 1998, Cryan et al. 2000, Miles et al. 2006) are still rare. Furthermore, information is limited on the comprehensive effects of landscape structure and composition on roost selection for an entire bat community.

Our objectives were to 1) identify landscape features that were important to roost selection by a forest-dwelling bat community, including topography, forest habitat class, and landscape structure; 2) determine whether commonalities existed in response to landscape metrics among bat species; 3) evaluate how changes in scale of measurement affected associations between roost locations and landscape attri-

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butes; and 4) develop potential a priori models relating landscape features to bat roosting that can be tested in future studies. To address these objectives, we created logistic regression models to differentiate areas selected for roosting from random areas. We also modeled roost selection at 2 spatial scales to determine how relationships between landscape elements and roost selection were affected by changes in scale. We examined roost selection by 6 bat species: big brown (*Eptesicus fuscus*), evening (*Nycticeius humeralis*), northern long-eared (*Myotis septentrionalis*), eastern red (*Lasiurus borealis*), Seminole (*Lasiurus seminolus*), and eastern pipistrelle (*Perimyotis subflavus*) that occurred sympatrically in a diversely managed forest.

## STUDY AREA

We conducted our study in the 6,545-ha Upper Lake Winona Basin, situated in the Ouachita Mountains of central Arkansas, USA (34°48′N, 92°58′W). The Ouachita Mountains consisted of east–west oriented ridges where elevation was 152–853 m, mean annual precipitation ranged from 112 cm to 137 cm, and mean annual temperature ranged from 13.9° C to 16.1° C (Skiles 1981).

The study area was completely forested; no farms, houses, agricultural lands, or pastures existed in the study portion of the basin. Most of the basin consisted of mixed shortleaf pine (*Pinus echinata*)–hardwood forests managed by the Forest Service, United States Department of Agriculture (Ouachita National Forest; ONF). The basin also contained a mix of other forest types, primarily oak (*Quercus* spp.)–hickory (*Carya* spp.). Intensively managed industrial timberlands (owned by Weyerhaeuser Company) accounted for 12% (778 ha) of the area. Those lands consisted primarily of closed canopy and thinned loblolly pine (*Pinus taeda*) plantations managed under a 30–35-year rotation (Perry et al. 2007).

National forestlands within the basin were divided into 6 management blocks (513–1,791 ha) where different silvicultural treatments were implemented in 2000. Blocks included pine–woodland restoration (1,232 ha); single-tree selection (864 ha); group selection (1,044 ha); mixed management (1,791 ha); and a mostly untreated block, which consisted primarily of mature, second-growth, pine–hardwood forest (836 ha; Perry et al. 2007). Throughout the basin, stands (16–90 ha) that were either inoperable (e.g., slopes >35%), in regeneration (typically <50 yr 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, seral stages, ownership, and treatment history the basin contained most of the predominant forest types, aspects, and forest-management practices that existed in the Ouachita Mountains.

## METHODS

### Bat Capture and Radiotelemetry

From mid-May to late July 2000–2005, we captured bats with mist nets at 21 trapping locations distributed throughout the basin. Trapping locations were primarily stream pools, but they included forest roads, ponds, and dry creek beds. We recorded bat species, mass, sex, and age (juv or ad; Racey 1974) for all captures. We followed the guidelines of the American Society of Mammalogists for the capture, handling, and care of mammals (Animal Care and Use Committee 1998).

We used 0.24–0.71-g radiotransmitters (Blackburn Transmitters, Nacogdoches, TX, and Holohil Systems Limited, Carp, ON, Canada) depending on bat species, with 10–21-day battery life, to locate bats at their diurnal roost sites from mid-May to early August. We attached transmitters to the mid-scapular region with Skin Bond® surgical adhesive (Smith & Nephew, Inc., Largo, FL). Transmitter load was generally <5% of body mass (Aldridge and Brigham 1988). We tracked each bat to its roost site the morning after capture and about 5 days per week until its signal was lost. To ensure locations were as accurate as possible, we visually located most bats in their roosts. We collected Global Positioning System (GPS) coordinates for each bat roost using GPS receivers with accuracy ±10 m.

### Vegetation and Topography Mapping

We conducted spatial analyses in ArcView® 3.2 and ArcMap® 8.3. We obtained digital maps of forest stand boundaries from ONF. We updated and corrected stand boundaries using 10-m digital color orthoquads (DOQs) as templates. We classified forest stands based on the Continuous Inventory of Stand Condition database; we updated those data by ground-truthing, and we used tree core data from most stands to verify stand ages. We digitized boundaries of habitat classes on industrial timberlands from 10-m DOQs and classified those data with ground-truthing.

We classified each stand into one of 12 forest habitat classes based on stand age, silviculture treatment, and forest type (Table 1; Perry et al. 2007). We combined silviculture treatments that resulted in forest stands with similar vertical and spatial structure. Thus, we combined single-tree selection stands and pine–woodland restoration areas, which were initially treated with similar thinning, midstory removal, and burning in 2000, into a "thinned mature" class. On industrial timberlands, we used 2 habitat classes for plantations: closed canopy plantations and older thinned plantations (Table 1), but we excluded young open clearcuts (<10 yr old) because they made up <0.5% of available habitat.

We included elevation, slope, distance to streams, and distance to roads in analyses as topographic features. No paved roads existed within the basin; primary roads were gravel and infrequently traveled and secondary roads included gated roads, recently closed roads, and 4-wheel drive trails. We obtained data layers for roads and streams from ONF, and updated those data using DOQs. We collected locations of secondary roads either by digitizing from DOQs or by GPS. Stream data layers included ponds, which were relatively uncommon, <0.5 ha, and created as a water source for wildlife and fire fighting.

**Table 1.** Forest habitat classes[a] included in logistic regression models of roost selection by forest bats in the Ouachita Mountains of central Arkansas, USA, 2000–2005.

| Habitat class | Description |
|---|---|
| Pine <15 yr | Even-aged pines, <15 yr old |
| Pine 15–29 yr | Even-aged pines, 15–29 yr old |
| Hardwood 50–99 yr | Hardwood stands, primarily even-aged, 50–99 yr old |
| Hardwood ≥100 yr | Hardwood stands ≥100 yr old |
| PH[b] 30–49 yr | Mixed pine–hardwood stands, primarily even-aged, 30–49 yr old |
| PH 50–99 yr | Mixed pine–hardwood stands, primarily even-aged, 50–99 yr old |
| PH ≥100 yr | Mixed pine–hardwood stands, ≥100 yr old |
| Group selection | Mature mixed pine-hardwood stands that had undergone mostly recent group selection harvest and matrix thinning |
| Thinned mature | Mature (>50 yr 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 thinned to 13.8 $m^2$/ha overstory basal area |
| Seedtree | Pine seed tree cuts, open stands with scattered mature pines left for seed production |
| Industrial timberlands | |
| Closed plantation | Closed canopy loblolly pine plantations, approx. 14–25 yr old |
| Thinned plantation | Older and thinned loblolly pine plantations, approx. 20–35 yr old |

[a] See Perry et al. (2007) for details on silviculture treatments.
[b] PH = mixed pine and hardwood.

## Data Analysis

We generated a set of random locations for comparison with roost locations. To determine the area of available habitats where random locations were generated, we created a concave polygon that encompassed the outermost roosts in the study area and we considered that polygon the area of habitat available to bats. We created separate availability polygons for each species of bat. Within those polygons, we randomly generated 2 locations for each individual bat included in analyses.

Landscape structure and function possess inherent scales at which identifiable processes occur (Carlile et al. 1989, Turner 1989, Turner et al. 1989). However, justifying a biologically appropriate scale at which to model roost selection by forest bats is currently limited by a lack of empirical or theoretical knowledge. Therefore, we modeled relationships between locations of roosts and landscape metrics at 2 spatial scales to determine how those relationships were affected by changes in scale. We quantified patch configuration and the quantity of each habitat in 250-m and 1,000-m radii surrounding each random and roost location. We considered the 1,000-m radius similar in scale to habitat-use area. Although limited information is available on home-range size of many forest bats in the southeastern United States, the 1,000-m radius corresponded roughly with the average maximum distance traveled by red bats during foraging in forests of the southeastern United States (Elmore et al. 2005) and the average distance (1,137 m) between roost locations and foraging areas for eastern pipistrelles (Krishon et al. 1997). We used the 250-m radius to provide insight on site-specific locations of roosts.

At each roost and random location, we clipped a 250- and 1,000-m radius (19.6 ha and 314.2 ha, respectively) from vegetation maps. We then calculated landscape patch metrics (Table 2) and the total area of each forest habitat class (Table 1) within the 2 radii using Patch Analyst Grid (McGarigal and Marks 1995, Elkie et al. 1999). Because composition of the landscape changed during the study due to additional timber harvesting and aging of stands, we calculated separate landscape patch metrics and area of forest habitat classes for 3 time periods (2000–2002, 2003, and 2004–2005) that coincided with major changes in stand age classes and additional harvest treatments. We calculated the minimum straight-line distance from each roost and random location to the nearest road and stream. Distances from roosts and random points to the nearest road or stream included roads and streams that fell outside availability polygons. We used a 10-m digital elevation model of the study area to determine elevation and slope at each roost location and random location.

Individual bats frequently roosted at different sites within the same general area (usually the same stand) over multiple days; thus, roost locations for individuals were not spatially independent. To eliminate this spatial autocorrelation, we considered individual bats the experimental unit; we averaged landscape metrics for each bat and used these averaged values as the experimental unit. Although differences may occur in site selection between sexes of the same species (e.g., Cryan et al. 2000, Encarnação et al. 2005, Perry and Thill 2007*c*), sample size was not large enough for most species to conduct analysis by sex; therefore, we combined sexes for 4 of 6 species. We captured no female Seminole bats during the summer and only 3 female (all juvenile) evening bats, which we did not instrument. We included both sexes in models for big brown bats, northern long-eared bats, red bats, and pipistrelles, and most (69%) female roosts for these species were maternity.

For each species, we created a small- and large-scale logistic regression model to determine the best set of factors among forest habitat classes, patch configuration, and topographic metrics that predicted occurrence of roosts. We used conditional logistic regression, stratified by time periods, to account for year effects (Hosmer and Lemeshow 2000). Elevation, slope, and distance to nearest road or stream were not scale-dependent; thus, we included those measurements in both scale-dependent models.

**Table 2.** Patch configuration and topographic metrics included in logistic regression models of roost selection by forest bats in the Ouachita Mountains of central Arkansas, USA, 2000–2005.

| Landscape metric | Description |
|---|---|
| NUMP | Total no. of patches in a designated landscape area (no.) |
| PR | Patch richness; no. of patch types (no.) |
| MPS | Mean patch size in the landscape region (ha) |
| PSCOV[a] | Patch size CV = patch size SD/mean patch size (%) |
| IJI[a] | Interspersion juxtaposition index; measurement of patch adjacency; range from 0 (uneven distribution) to 100 (all patches are equally adjacent; %) |
| SDI[a] | Shannon's diversity index for patch types |
| SEI[a] | Shannon's evenness index for patch types |
| LPI[a] | Largest patch index; % of landscape composed of the largest patch (%) |
| TE | Total edge length (m) |
| Elevation | Elevation from digital elevation model (m above mean sea level) |
| Slope | Slope from digital elevation model (%) |
| Distance to streams | Straight-line distance to nearest stream (m) |
| Distance to roads | Straight-line distance to nearest road (m) |

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

Unlike many other animals for which researchers have accumulated substantial information on ecology and habitat associations, little information is available on habitat associations for many forest bats (e.g., eastern pipistrelles). Furthermore, creating a set of competing a priori models based on the biology of species was problematic because little information is available on roost placement in relation to patch configuration, most forest types, and many seral stages. Therefore, we used an exploratory method to determine a set of candidate models for each species of bat and scale using 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 2000). Because many patch-configuration metrics were highly correlated ($r \geq 0.70$), we included only 9 patch metrics (Table 2). We included 4 topographic metrics (Table 2) and 12 habitat variables (Table 1). To reduce the likelihood of overfitting models, we constrained the maximum number of variables allowed in candidate models such that ≥10 observations (including random locations) had to be present for each variable included in the model (Peduzzi et al. 1996). To reduce the influence of independent variables with imprecise or erroneous estimates, we 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).

We determined the most parsimonious models among all candidate models based on values of Akaike's Information Criterion (AIC) modified for small samples ($AIC_c$; Burnham and Anderson 2002). We used multimodel inference by averaging parameter estimates of models within 2 units of $AIC_{min}$; we used weights calculated among all models within 2 units of $AIC_{min}$ for weighted averages, and we calculated odds ratios (odds of roost location/odds of random location) from averaged parameters (Burnham and Anderson 2002). We calculated weighted unconditional standard errors for averaged parameter estimates (Burnham and Anderson 2002). For each parameter, we determined relative importance among all species using averaged models; importance was based on sums of Akaike weights (Burnham and Anderson 2002). Because importance was determined among averaged models for different species, relative importance values >1 were possible. We evaluated model strength using a generalized coefficient of determination (maximum-rescaled $R^2$; Nagelkerke 1991).

**Table 3.** Numbers of individual bats (by sex) and numbers of diurnal summer roosts for 6 species of bat included in logistic regression models of roost selection in the Ouachita Mountains of central Arkansas, USA, 2000–2005.

| | No. of individuals | | No. of roosts/individual | | |
|---|---|---|---|---|---|
| Species | M | F | Range | $\bar{x}$ | Total no. of roosts |
| Big brown bat | 12 | 4 | 1–5 | 2.1 | 34 |
| Northern long-eared bat | 21 | 21 | 1–7 | 2.4 | 102 |
| Evening bat | 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 |

# RESULTS

From 2000 to 2005, we located 426 roosts for 162 individuals of 6 species (Table 3). Most individuals included in model synthesis were adults. Juveniles made up 7% of red bats, 14% of northern long-eared bat, and 14% of eastern pipistrelle bats. All evening, Seminole, and big brown bats were adults.

## Species-Specific Responses

For big brown bats at the 250-m scale, $R^2 = 0.55$ for the most parsimonious logistic model relating landscape attributes to presence of roosts, and one model was within 2 units of $AIC_{min}$ (Appendix). At the 1,000-m scale, $R^2 = 0.35$ for the most parsimonious model, and 3 additional models were within 2 units of $AIC_{min}$. At both scales, averaged models indicated that this species was more likely to roost in areas of less slope, higher elevation, closer to streams, and in areas containing more group selection than random locations (Table 4). At the 250-m scale, roosts had a greater likelihood of occurring in areas that contained lower amounts of pine 15–29 years old than random, and at the 1,000-m scale, roosts were more likely to be in regions of the basin with greater amounts of older (≥100-yr-old) hardwoods. In general, big brown bats were more likely to roost in relatively flat upland areas of the basin, near upland streams, and in areas containing partially harvested or unharvested mature stands. Most roosts were in thinned

**Table 4.** Model-averaged parameter estimates, weighted unconditional standard errors, and odds ratios for logistic regression models comparing landscape attributes surrounding diurnal summer roosts with random locations at 2 spatial scales for 6 bat species in the Ouachita Mountains of central Arkansas, USA, 2000–2005.

| Bat species and parameter | Spatial scale | | | | | |
|---|---|---|---|---|---|---|
| | 250 m | | | 1,000 m | | |
| | Estimate | SE | Odds[a] | Estimate | SE | Odds[a] |
| Big brown bat | | | | | | |
| Pine 15–29 yr[b] | −0.505 | 0.524 | 0.604 | | | |
| Hardwood ≥100 yr | | | | 0.181 | 0.140 | 1.198 |
| Group selection | 0.330* | 0.149 | 1.391 | 0.002 | 0.002 | 1.002 |
| Elevation | 0.065* | 0.025 | 1.067 | 0.037* | 0.018 | 1.038 |
| Slope | −0.118 | 0.071 | 0.889 | −0.122 | 0.063 | 0.885 |
| Distance to streams[c] | −0.011 | 0.007 | 0.989 | −0.003 | 0.003 | 0.997 |
| Northern long-eared bat | | | | | | |
| Pine 15–29 yr | −0.105 | 0.074 | 0.900 | | | |
| PH ≥100 yr | | | | 0.032* | 0.011 | 1.033 |
| PH 50–99 yr | | | | −0.023* | 0.006 | 0.978 |
| Seedtree | | | | 0.062* | 0.030 | 1.064 |
| Group selection | 0.007 | 0.011 | 1.007 | | | |
| Thinned mature | 0.068* | 0.028 | 1.070 | | | |
| Closed plantation | | | | −0.031* | 0.013 | 0.970 |
| Slope | 0.079* | 0.030 | 1.082 | | | |
| Distance to roads | −0.005* | 0.002 | 0.995 | | | |
| NUMP | | | | −0.016 | 0.019 | 0.984 |
| TE | | | | 0.001 | 0.001 | 1.001 |
| IJI | | | | 0.012 | 0.012 | 1.012 |
| LPI | | | | 0.022 | 0.018 | 1.022 |
| Evening bat | | | | | | |
| Hardwood 50–99 yr | 0.336 | 0.180 | 1.399 | 0.038* | 0.019 | 1.039 |
| PH 50–99 yr | | | | −0.016* | 0.008 | 0.984 |
| Hardwood ≥100 yr | | | | 0.077 | 0.098 | 1.081 |
| Group selection | 0.282* | 0.141 | 1.326 | | | |
| Thinned mature | 0.256* | 0.089 | 1.292 | | | |
| Distance to streams | | | | −0.001 | 0.001 | 0.999 |
| Closed plantation | | | | −0.025 | 0.015 | 0.976 |
| MPS | −0.310 | 0.164 | 0.733 | | | |
| NUMP | −0.383 | 0.329 | 0.682 | | | |
| Eastern red | | | | | | |
| PH ≥100 yr | 0.124 | 0.095 | 1.132 | | | |
| Group selection | 0.071 | 0.037 | 1.074 | | | |
| Seedtree | | | | −0.051 | 0.040 | 0.950 |
| PH 30–49 yr | −0.040 | 0.051 | 0.961 | | | |
| Pine 15–29 yr | | | | −0.001 | 0.001 | 0.999 |
| Distance to roads | −0.003 | 0.002 | 0.997 | −0.003* | 0.002 | 0.997 |
| SDI | −1.441* | 0.573 | 0.237 | | | |
| PSCOV | | | | −0.003 | 0.003 | 0.997 |
| LPI | | | | 0.033 | 0.024 | 1.034 |
| TE | | | | 0.001 | 0.001 | 1.001 |
| Seminole | | | | | | |
| Hardwood 50–99 yr | | | | −0.118* | 0.046 | 0.889 |
| PH 50–99 yr | | | | −0.053* | 0.020 | 0.948 |
| Pine <15 yr | | | | −0.725 | 0.431 | 0.484 |
| Hardwood ≥100 yr | | | | −0.041* | 0.018 | 0.960 |
| Thinned mature | 0.099 | 0.065 | 1.104 | | | |
| Slope | −0.022 | 0.024 | 0.978 | | | |
| Distance to streams | −0.012* | 0.004 | 0.988 | | | |
| PR | | | | −1.403* | 0.582 | 0.246 |
| TE | −0.003* | 0.001 | 0.997 | | | |

mature (52.9%) or group selection stands (26.5%; Perry et al. 2007), and all roosts were in pine snags.

For northern long-eared bats at the 250-m scale, $R^2 = 0.29$ for the most parsimonious logistic model relating landscape attributes to presence of roosts, and 2 additional models were within 2 units of $AIC_{min}$ (Appendix). At the 1,000-m scale, $R^2 = 0.35$ for the most parsimonious model and 4 additional models were within 2 units of $AIC_{min}$. At the

**Table 4.** Continued.

| Bat species and parameter | 250 m Estimate | 250 m SE | 250 m Odds[a] | 1,000 m Estimate | 1,000 m SE | 1,000 m Odds[a] |
|---|---|---|---|---|---|---|
| Eastern pipistrelle | | | | | | |
| Pine 15–29 yr | −0.087 | 0.088 | 0.917 | −0.025* | 0.012 | 0.975 |
| Pine <15 yr | | | | 0.048 | 0.045 | 1.050 |
| Hardwood 50–99 yr | 0.217* | 0.083 | 1.242 | | | |
| Hardwood ≥100 yr | | | | 0.667 | 0.373 | 1.948 |
| PH 50–99 yr | | | | −0.015* | 0.007 | 0.985 |
| PH ≥100 yr | 0.399* | 0.143 | 1.490 | | | |
| Group selection | 0.237* | 0.095 | 1.267 | | | |
| Thinned mature | 0.178* | 0.065 | 1.195 | −0.008 | 0.005 | 0.992 |
| Distance to roads | 0.004 | 0.002 | 1.004 | 0.002 | 0.002 | 1.003 |
| PR | 0.412 | 0.327 | 1.509 | | | |
| LPI | 0.014 | 0.013 | 1.014 | 0.075* | 0.023 | 1.078 |
| IJI | | | | 0.140* | 0.058 | 1.150 |
| PSCOV | 0.003 | 0.003 | 1.003 | | | |

[a] Comparison of roost sites with random locations: odds = odds ratio for presence of roosts (odds roost/odds random).
[b] For definitions of parameters, see Tables 1 and 2.
[c] Because roads and streams were distance measures, – indicates roosts were more likely to be closer to these landscape features than random.
* 95% CIs for parameter estimates did not contain zero.

250-m scale, the averaged model indicated this species was more likely to roost in areas containing abundant thinned mature forest and group selection, but lower amounts of pine 15–29 years old (Table 4). Furthermore, roosts of northern long-eared bats were more likely closer to roads and in areas with greater slope than at random locations. At the 1,000-m scale, the parameter-averaged model indicated roosts were more likely to be in regions of the basin that had abundant pine seed tree stands and lower amounts of closed canopy pine plantations. Although many (22.5%) roosts were in unthinned stands of mixed pine–hardwood 50–99 years old (Perry et al. 2007), at the 1,000-m scale northern long-eared bats were associated with areas containing lower amounts of that habitat type. At the larger scale, roosts were associated with areas having fewer number of patches (NUMP), more edge (TE), greater interspersion index (IJI), and greater largest patch index (LPI) than random. In general, northern long-eared bats roosted in steeper regions of the basin that were managed with partial or no harvest, and away from areas dominated by dense young forests. Seventy-one percent of northern long-eared bat roosts were in pines, and 90% of roosts were in snags (Perry and Thill 2007*c*).

For male evening bats at the 250-m scale, $R^2 = 0.44$ for the most parsimonious logistic model relating landscape attributes to roosts locations (Appendix). At the 1,000-m scale, $R^2 = 0.35$ for the most parsimonious model and 2 additional models were within 2 units of $\mathrm{AIC}_{\mathrm{min}}$ (Appendix). At the 250-m scale, the averaged model indicated roosts of male evening bats were more likely located in areas containing greater amounts of hardwood 50–99 years old, group selection, and thinned mature forest than random locations (Table 4). Furthermore, roost locations were more likely to be in areas dominated by smaller patches (MPS) and a lower overall number of patches (NUMP). At the 1,000-m scale, averaged models indicated that roosts of male evening bats were more likely to be in areas containing hardwood 50–99 years old and hardwood ≥100 years old, but less closed canopy pine plantation than random locations; roosts were located closer to streams than random. Although many (19.1%) roosts were in stands of mixed pine–hardwood 50–99 years old (Perry et al. 2007), roosts were more likely to be in areas containing less of that habitat at the 1,000-m scale. Generally, male evening bats roosted in areas that contained abundant partially harvested pine–hardwood stands interspersed with stands of unharvested hardwood that were close to streams, but bats were less likely to roost in portions of the study area dominated by continuous forests of unmanaged mixed pine–hardwood. Most (57.4%) roosts were in thinned mature stands (Perry et al. 2007); 39% of roosts were in pines, 63% were in hardwoods, and 63% were in snags.

For eastern red bats at the 250-m scale, $R^2 = 0.19$ for the most parsimonious logistic model relating landscape attributes to presence of roosts, and 2 additional models were within 2 units of $\mathrm{AIC}_{\mathrm{min}}$ (Appendix). At the 1,000-m scale, $R^2 = 0.10$ for the most parsimonious model, and 5 additional models were within 2 units of $\mathrm{AIC}_{\mathrm{min}}$. At the 250-m scale, the averaged model indicated red bats were more likely to roost in areas containing greater amounts of group selection and older (≥100 yr old) forests of mixed pine–hardwood and lower amounts of immature (30–49 yr old) mixed pine–hardwood than random locations (Table 4). Furthermore, roosts were associated with areas of lower diversity (SDI). At both scales, red bats roosts were closer to roads than random. At the 1,000-m scale, roosts of red bats were more likely in areas containing lower amounts of seed tree harvesting and pine 15–29 years old than random and were in areas dominated by larger patches (LPI), with more edge (TE), and less variability in patch size (PSCOV). Most roosts were in thinned mature stands (28.3%) or unharvested stands of mixed pine–hardwood 50–99 years old (24.8%; Perry et al. 2007) and 98% of roosts were in foliage of hardwoods.

For male Seminole bats at the 250-m scale, $R^2 = 0.60$ for the most parsimonious logistic model relating landscape attributes to presence of roosts, and one additional model was within 2 units of $\mathrm{AIC}_{\mathrm{min}}$ (Appendix A). At the 1,000-m scale, $R^2$ for the most parsimonious model was 0.74, and no other models were within 2 units of $\mathrm{AIC}_{\mathrm{min}}$. At the 250-m scale, roosts of male Seminole bats were more likely located in areas with greater amounts of thinned mature habitat, less edge (TE), less slope, and closer to streams than random (Table 4). At the 1,000-m scale, roosts of male Seminole bats were more likely in areas with less unthinned forests of mixed pine–hardwood or hardwood 50–99 years old, less hardwood ≥100 years old, less pine <15 years old, and lower patch richness (PR) than random. In general, male Seminole bats roosted in homogeneous areas of thinned forests that contained abundant pines and few hardwoods, that were near streams, and in areas with little slope. Most roosts (60.8%) were in thinned mature stands and they rarely roosted in unthinned forests; all roosts were in foliage of live trees, and 95% of roosts were in pines (Perry and Thill 2007*b*).

For eastern pipistrelles at the 250-m scale, $R^2 = 0.52$ for the most parsimonious logistic model relating landscape attributes to presence of roosts, and 3 other models were within 2 units of $\mathrm{AIC}_{\mathrm{min}}$ (Appendix). At the 1,000-m scale, $R^2 = 0.47$ for the most parsimonious model and 3 additional models were within 2 units of $\mathrm{AIC}_{\mathrm{min}}$ (Appendix). At the 250-m scale, the averaged model indicated pipistrelles were more likely to roost in areas containing more group selection and hardwood 50–99 years old, mixed pine–hardwood ≥100 years old, greater patch richness, and variability in patch size (PSCOV) than random (Table 4). At both scales, roosts were more likely located in areas with lower amounts of pine 15–29 years old, greater LPI, and further from roads than random. At the 1,000-m scale, roosts were more likely to be in areas with less mixed pine–hardwood 50–99 years old, more pine <15 years old, more hardwood ≥100 years old, and greater interspersion (IJI) of patch types than random. Oddly, thinned mature habitats had a positive effect at the small scale, but a negative effect at the large scale. In general, eastern pipistrelles were associated with areas containing mature stands with a hardwood component and a good interspersion of diverse patch types and sizes. Most roosts were located in unharvested 50–99-year-old stands of mixed pine–hardwood (22.4%) or hardwood (34.7%; Perry et al. 2007), and all roosts were in tree foliage (Perry and Thill 2007*a*).

### Summary of Parameters Included in Models

Among all species, 7 parameters that were included in models generally had a positive influence on roost selection, 8 had a mixed effect, 8 had mostly inverse effects, and 2 were not included in any models (Table 5). Amount of group selection and thinned mature forest, distance to streams, and LPI were included most often in models as a positive influence on roost selection. Amount of immature pine 15–29 years old and mixed pine–hardwood 50–99 years old were the most often included parameters with inverse relationships with roost selection. Thinned plantation and Shannon's evenness index of patch types (SEI) were not included in any models. Based on importance values, the 2 parameters with the highest importance values at the small scale were group selection and thinned mature (Table 5). At the large scale, the 2 most important parameters were hardwoods ≥100 years old and mixed pine–hardwood 50–99 years old. Mean importance of forest-habitat classes was 1.12 (± 0.45 SE) at the small scale and 1.46 (± 0.36) at the large scale, mean importance of topographic metrics was 2.08 (± 0.40) at the small scale and 1.08 (± 0.18) at the large scale, and mean importance of patch metrics was 0.49 (± 0.14) at the small scale and 0.68 (±0.28) at the large scale.

## DISCUSSION

### Scale

Land ownership, historical land uses, and topoedaphic factors can create associations between topography and habitats that are infrequently addressed in landscape studies. In general, forest cover and management patterns differed throughout our study area according to slope, aspect, soils, and ownership; these fundamentally different regions were aggregated into larger blocks than typical stand sizes (16–18 ha). Lowland areas (more fertile) were historically owned and managed by Weyerhaeuser Company using intensive even-aged silviculture. That region was dominated by closed canopy and thinned loblolly pine plantations. Regions of the basin with moderate slope and south-facing aspects were primarily natural pine forests and were managed by the United States Forest Service (USFS) for timber production; these areas included substantial amounts of partial harvesting. Areas too steep (generally >35%) for logging were typically mature or older forests with little silvicultural activity. Thus, the larger scale analysis (1,000-m) generally characterized roost selection among these broad categories of management, whereas the small scale (250 m) was more indicative of site selection within these broader areas of management. Some species (e.g., northern long-eared bats and big brown bats) tended to roost more in upland areas dominated by USFS land ownership, natural stands, or uneven-aged management, whereas others (such as red bats) roosted throughout the basin.

Small-scale models were generally more powerful than large-scale models at describing relationships between landscapes and roost selection (average $R^2$ values were 8% higher in small-scale models than in large-scale models). For most species, parameters included in models differed between the 2 scales. For Seminole bats and northern long-eared bats, small-scale and large-scale models shared no common parameters. Both large- and small-scale models contained preferred and avoided roosting habitats. For example, the small-scale model for northern long-eared bats

**Table 5.** Number of species-specific models that contained each parameter (grouped by general effect on roost selection), influence (+ or −) of each parameter, and relative interspecies importance (based on sums of Akaike wt) on roost selection by 6 species of forest bat measured at 2 spatial scales in the Ouachita Mountains of central Arkansas, USA, 2000–2005.

| | 250-m scale | | 1,000-m scale | |
|---|---|---|---|---|
| Parameter | No. models | Importance | No. models | Importance |
| Mostly positive | | | | |
| Group selection[a] | + + + + +[b] | 4.23 | + | 0.21 |
| Thinned mature | + + + + | 3.84 | − | 1.00 |
| LPI | + | 0.34 | + + + | 2.52 |
| Distance to streams | + + | 2.00 | + + | 0.75 |
| PH ≥100 yr | + + | 1.65 | + | 1.00 |
| IJI | | 0.00 | + + | 1.31 |
| Elevation | + | 1.00 | + | 1.00 |
| Mixed | | | | |
| Distance to roads | − + + | 2.84 | − + | 1.60 |
| Hardwood 50–99 yr | + + | 1.84 | − + | 2.00 |
| Hardwood ≥100 yr | | 0.00 | − + + + | 3.21 |
| TE | − | 1.00 | + + | 0.91 |
| Seedtree | | 0.00 | − + | 1.67 |
| Pine <15 yr | | 0.00 | − + | 1.35 |
| PSCOV | + | 0.24 | − | 0.26 |
| PR | + | 0.35 | − | 1.00 |
| Mostly inverse | | | | |
| Pine 15–29 yr | − − − | 1.61 | − − | 1.10 |
| PH 50–99 yr | | 0.00 | − − − − | 4.00 |
| Slope | − − + | 2.48 | − | 1.00 |
| Closed plantation | | 0.00 | − − | 2.00 |
| NUMP | − | 0.48 | − | 0.13 |
| MPS | − | 1.00 | | 0.00 |
| SDI | − | 1.00 | | 0.00 |
| PH 30–49 yr | − | 0.26 | | 0.00 |
| No relationship | | | | |
| SEI | | 0.00 | | 0.00 |
| Thinned plantation | | 0.00 | | 0.00 |

[a] For definitions of parameters, see Tables 1 and 2.

[b] Each + indicates this parameter was included in an averaged model for one species and had a positive relationship with roost selection, − indicates an inverse relationship, and blank spaces indicates the parameter was not included in any models. For distance to roads and streams, signs of parameter estimates were changed to indicate if proximity had a positive effect (+) or negative effect (−) on roost placement.

included a positive association with thinned mature habitats, whereas the large-scale model included positive associations with mixed pine–hardwood ≥100 years old and seed tree stands; these associations are reflective of stand-level habitat preferences derived from Euclidean-distance analyses (Perry et al. 2007). Thus, both small- and large-scale models each contained parameters that were potentially important to roost selection in bats.

Roost selection within a landscape is likely affected by attributes beyond those of the stand selected for roosting, but effects of many landscape attributes may differ according to scale of measurement (scale dependency). For example, habitats that contained the greatest numbers of roosts, including thinned mature and group selection (Perry et al. 2007), were more often included as positive associations in small-scale models. Thus, small-scale models were likely more reflective of stand-level habitat selection, whereas parameters included in large-scale models may be more important to other aspects of bat ecology, such as foraging. Because the 1,000-m scale was similar in scale to home-range size for many bat species, that area likely included most of the habitats required for the daily needs of individuals. Proximity to water sources, flight corridors, and foraging areas, as well as predator densities, frequency of human disturbance, and topographic microclimate could potentially affect the selection process within a landscape.

## Forest Habitats

Forest habitat classes were typically included more often than patch configuration or topography in models differentiating roost from random locations, suggesting roost selection may be influenced more by habitat attributes (e.g., forest type and seral stage) than other features of the landscape. Because we created forest habitat classes based on differences in forest structure that would potentially affect roosting microhabitat, it is not surprising that habitat classes had a strong influence on roost locations. Studies of bat activity suggest that microhabitat or stand-level effects are typically stronger than landscape-level effects (Gehrt and Chelsvig 2003, Ford et al. 2006, Loeb and O'Keefe 2006).

Many species roosted in areas containing abundant uncluttered forest that resulted from recent management (thinning, partial harvest, and burning). Group selection and thinned mature habitats had the highest positive importance values among all parameters in small-scale models. Based on averaged models at the small scale, northern long-eared bats, evening bats, Seminole bats, and eastern pipistrelles had a positive association with areas containing recently thinned mature forest and all species except Seminole bats demonstrated a positive association with areas containing abundant recently harvested group selection. These partially harvested areas retained the mature overstory pines and hardwoods used by many species for roosting but had reduced vertical clutter. Perry et al. (2007), using Euclidean distance analysis and a different definition of available habitat, found a similar affinity for roosting in (or close to) partially harvested or thinned forest stands for most species in this landscape. Other studies suggest some bat species prefer roosting in stands with relatively lower tree density or canopy coverage (e.g., Vonhof and Barclay 1996, Hutchinson and Lacki 2000, Kalcounis-Rüppell et al. 2005, Boyles and Aubrey 2006, Psyllakis and Brigham 2006). Furthermore, activity of many species is generally greater in less-cluttered habitats such as thinned stands (e.g., Erickson and West 1996, Menzel et al. 2002, Owen et. al. 2004), where open-forest conditions may facilitate flight and foraging. Thus, presence of naturally or silviculturally derived stands with reduced vertical structure and abundant overstory trees may prevail over other aspects of the landscape in affecting roost location for many forest bats, especially at smaller scales. In contrast, species such as eastern pipistrelles may roost more in mature, closed canopy forests with an abundant hardwood midstory, but they tend to roost in proximity to open forest habitats (Perry and Thill 2007*a*). Although bats frequently roosted in stands of mixed pine–hardwood forest 50–99 years old, areas of the basin that contained large homogeneous blocks of second-growth forest under limited management (such as the unharvested block) were used less for roosting than the more diversely forested areas.

The big brown bat, northern long-eared bat, and evening bat are cavity- and crevice-roosting species that relied greatly on snags for roosting (e.g., Rabe et al. 1998, Miles et al. 2006, Perry and Thill 2007*c*). Although we generated random locations geographically and without regard to available structures such as snags, it was unlikely most areas were lacking in snags because a widespread ice storm in winter 2000–2001 created abundant snags throughout the basin.

### Topographic Metrics

Distance to streams was included in 2 small-scale models and 2 large-scale models, and it was a positive influence on roost selection for big brown bats, evening bats, and Seminole bats. Distance to water is often found to influence roost selection (Kalcounis-Rüppell et al. 2005). The importance of riparian areas to bats is well documented, providing both high-quality foraging and drinking areas (e.g., Grindal et al. 1999, Seidman and Zabel 2001, Menzel et al. 2005).

Distance to roads was included in 3 small-scale averaged models and 2 large-scale models. Roosts of red bats were more likely to be closer to roads than random locations at both scales, and northern long-eared bats were more likely to roost closer to roads than random at the small scale. However, roosts of eastern pipistrelles were more likely to be further from roads than random locations at both scales. 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, 2 of the most common predators of birds and bird nests in the Ouachita Mountains, raccoons (*Procyon lotor*) and black rat snakes (*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. In contrast, studies suggest that roads provide flight corridors or navigational references for bats (e.g., Limpens and Kapteyn 1991, Walsh and Harris 1996), and some bat species tend to forage and commute in edge habitats more than forest interiors and open, nonforested areas (Ekman and de Jong 1996, Verboom and Huitema 1997, Grindal and Brigham 1999, Hogberg et al. 2002). Consequently, some bats may prefer to roost in proximity to travel corridors.

Roads seemed to have little effect on roost placement of big brown bats, evening bats, and Seminole bats, perhaps because so much of the study area had been recently thinned. Before thinning, roads would have offered the least cluttered travel corridors for bats. Alternatively, roads may not influence roost selection for some species. For example, morphological and vocalization characteristics of the eastern pipistrelle suggest it is adapted to navigating in cluttered habitats (Menzel et al. 2005); thus, it may use roads less than other species.

Locations of bat roosts may be influenced by elevation and slope in mountainous areas such as the western United States (Ormsbee and McComb 1998, Rabe et al. 1998, Baker and Lacki 2006). We found elevation was included only in models for big brown bats; they were more likely to roost at higher elevations than random. However, because differences in elevation in our study area were generally <400 m, affinity of big brown bats for higher elevation areas may have resulted from differences in vegetation or management associated with elevation and not climatic factors such as temperature.

Slope was included in models for 3 species. Because areas of greater slope were typically not harvested due to operability constraints, areas of gentle slope were typically dominated by pines, and they were subjected more often to partial harvest or intensive management. Some species (Seminole bat and big brown bat) roosted in areas of gentle slope, likely because partial harvesting and thinning was concentrated in those areas and these treatments created the open pine habitats where both species roosted extensively; 79% of big brown roosts and 84% of Seminole bats roosts were in partially harvested or thinned stands dominated by pine.

### Patch Configuration

Using mist nets, 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. For roosting, we found patch metrics were included more often in large- than in small-scale models. Furthermore, importance values of patch metrics were generally greater at the large scale (average = 0.68 ± 0.28 SE) than the small scale (0.49 ± 0.14).

Although forest landscape attributes commonly coincide with activity or presence of forest bats in agricultural areas that contain limited patches of forest (e.g., Gehrt and Chelsvig 2003, Murray and Kurta 2004), we expected responses to most landscape configuration metrics would be weak because the entire study area was forested (e.g., Ford et al. 2006, Loeb and O'Keefe 2006). Nonetheless, landscape patch configuration metrics were included in models for all species except big brown bats. The patch configuration parameter included most often in models was LPI, and it was included in models for northern long-eared bats, red bats, and eastern pipistrelles. Inclusion of this parameter suggested that these species were more likely to roost at sites dominated by a single large patch.

Effects of habitat diversity on roost locations differed among species; some species seemed to favor roosting at diverse sites and others seemingly roosted at homogeneous sites. At the small scale, eastern pipistrelles were more likely to roost at locations that provided greater habitat heterogeneity, with greater PR and PSCOV. Although eastern pipistrelles roosted mostly in unharvested patches of forest, they frequently roosted in small unharvested buffer strips along stream drains (greenbelts) within partially harvested stands (Perry et al. 2007, Perry and Thill 2007*a*). These partially harvested stands were aggregated in relatively large blocks (greater LPI), but they had greater within-stand diversity (e.g., greenbelts, group openings) than unharvested stands. In contrast, Seminole bats were more likely to roost in areas with lower patch richness (large scale) and lower amounts of edge (small scale), suggesting they roosted mostly in homogenous areas. Seminole bats roosted primarily in larger blocks of open forests that were dominated by pines and had little midstory; they rarely roosted in closed-canopy or unthinned forests, nor did they roost in greenbelts imbedded in thinned stands (Perry et al. 2007, Perry and Thill 2007*b*).

### Model Accuracy

Strength of models for most species was moderate to high ($R^2 \geq 0.30$), with the exception of models for red bats (small-scale $R^2$ range = 0.16–0.20; large-scale $R^2$ range = 0.05–0.12). Furthermore, 95% confidence intervals for most parameter estimates included in competing models (at both scales) for red bats contained zero, suggesting the usefulness of most parameters as predictors was low (Table 4). Small parameter effects and relatively low model strength suggest that red bats may be more of a habitat generalist than other species, as suggested by others (e.g., Hutchinson and Lacki 1999). In contrast, strength of models for male Seminole bats was relatively high (average small-scale $R^2 = 0.62$; large-scale $R^2 = 0.74$), and most confidence intervals for parameter estimates did not contain zero, possibly because this species may prefer a narrower range of habitats (Perry and Thill 2007*b*). The small scale model for big brown bats had a relatively high coefficient of determination (average $R^2 = 0.50$), but most confidence intervals for parameter estimates contained zero, suggesting that the overall model explained much of the variation but most individual parameters had little predictive power. Future studies that use our models or parameters for a priori model construction should take into account both model strength ($R^2$) and significance of parameter estimates.

Patch configuration metrics included in 2 models appeared contradictory. At the 1,000-m scale, greater TE and lower NUMP were both included in the model for northern long-eared roost sites. For evening bats at the 250-m scale, smaller MPS and lower number of patches were both included in the model. Reducing the number of patches should theoretically decrease edge and increase mean patch size in a defined area. Thus, we could not explain these contradictory parameters geometrically, and inclusion of some of those parameters may have been spurious.

## MANAGEMENT IMPLICATIONS

Because each species of bat differed somewhat in its response to landscape parameters and these responses varied at the scale of measure, a one-size-fits-all approach to managing a landscape for bats is likely inappropriate. Therefore, the importance of habitat diversity in areas of contiguous forest cannot be overemphasized. Large and small blocks of various forest types, homogenous and heterogeneous patterns of stand distribution, and proximity to roads each differed in their effects on different species. Our results suggest that a variety of stand types (pine and hardwood) and conditions (different successional stages and management treatments), varying in size and elevation and distributed in varying proximities to roads and water sources throughout a landscape, would likely provide the landscape components for roosting required to maintain a diverse community of forest bats in the Ouachita Mountains.

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**Appendix.** Akaike's Information Criterion for small samples (AIC$_c$), difference ($\Delta$AIC$_c$) between AIC$_c$ and the best-approximating model (AIC$_{\mathrm{min}}$), and AIC$_c$ weight ($w_i$)[a] for logistic regression models within 2 units of AIC$_{\mathrm{min}}$ comparing roost and random locations for 6 bat species at 2 spatial scales (250 m and 1,000 m) in the Ouachita Mountains of central Arkansas, USA, 2000–2005.

| | 250 m | | | | 1,000 m | | | |
|---|---|---|---|---|---|---|---|---|
| Bat species and parameters | AIC$_c$ | $\Delta$AIC$_c$ | $w_i$ | $R^2$ | AIC$_c$ | $\Delta$AIC$_c$ | $w_i$ | $R^2$ |
| Big brown bat | | | | | | | | |
| +[b]elevation −slope −streams[c] +GS −P15-29yr | 42.74 | 0.00 | 0.71 | 0.55 | | | | |
| +elevation −slope −streams +GS | 44.55 | 1.81 | 0.29 | 0.46 | | | | |
| +elevation −slope +H≥100yr −streams | | | | | 49.32 | 0.00 | 0.35 | 0.35 |
| +elevation −slope +H≥100yr | | | | | 49.78 | 0.46 | 0.27 | 0.28 |
| +elevation −slope +H≥100yr −streams +GS | | | | | 50.36 | 1.04 | 0.21 | 0.38 |
| +elevation −slope | | | | | 50.71 | 1.39 | 0.17 | 0.20 |
| Northern long-eared bat | | | | | | | | |
| +TM +slope −roads −P15-29yr | 128.12 | 0.00 | 0.51 | 0.29 | | | | |
| +TM +slope −roads | 129.49 | 1.38 | 0.26 | 0.26 | | | | |
| +TM +slope −roads −P15-29yr +GS | 129.70 | 1.58 | 0.23 | 0.30 | | | | |
| −PH50-99yr +PH≥100yr −CP +seedtree | | | | | 121.52 | 0.00 | 0.36 | 0.35 |
| −PH50-99yr +PH≥100yr −CP +seedtree +LPI +TE +IJI | | | | | 122.96 | 1.43 | 0.18 | 0.39 |
| −PH50-99yr +PH≥100yr −CP +seedtree +LPI +TE | | | | | 123.10 | 1.57 | 0.17 | 0.37 |
| −PH50-99yr +PH≥100yr −CP +seedtree +LPI | | | | | 123.18 | 1.65 | 0.16 | 0.35 |
| −PH50-99yr +PH≥100yr −CP +seedtree +LPI +TE + IJI −NUMP | | | | | 123.52 | 1.99 | 0.13 | 0.41 |
| Evening bat | | | | | | | | |
| +GS +H50-99yr +TM −MPS | 46.43 | 0.00 | 0.52 | 0.44 | | | | |
| +GS +H50-99yr +TM −MPS −NUMP | 46.58 | 0.15 | 0.48 | 0.49 | | | | |
| +H50-99yr −PH50-99yr −CP | | | | | 48.37 | 0.00 | 0.46 | 0.35 |
| +H50-99yr −PH50-99yr −CP +H≥100yr | | | | | 48.94 | 0.57 | 0.35 | 0.39 |
| +H50-99yr −PH50-99yr −CP +H≥100yr −streams | | | | | 50.15 | 1.78 | 0.19 | 0.42 |
| Eastern red bat | | | | | | | | |
| −SDI +GS −roads +PH≥100yr | 142.33 | 0.00 | 0.38 | 0.19 | | | | |
| −SDI +GS −roads | 142.51 | 0.18 | 0.35 | 0.16 | | | | |
| −SDI +GS −roads +PH≥100yr −PH30-49yr | 143.09 | 0.76 | 0.26 | 0.20 | | | | |
| −Roads +LPI −seedtree | | | | | 148.13 | 0.00 | 0.24 | 0.10 |
| −Roads +LPI | | | | | 148.33 | 0.19 | 0.21 | 0.08 |
| −Roads +LPI −seedtree +TE | | | | | 148.85 | 0.71 | 0.17 | 0.12 |
| −Roads +LPI −seedtree +TE −PSCOV | | | | | 148.88 | 0.75 | 0.16 | 0.14 |
| −Roads | | | | | 149.48 | 1.35 | 0.12 | 0.05 |
| −Roads +LPI −seedtree +TE −PSCOV −P15-29yr | | | | | 149.86 | 1.73 | 0.10 | 0.15 |
| Seminole bat | | | | | | | | |
| −TE +TM −streams | 37.04 | 0.00 | 0.52 | 0.60 | | | | |
| −TE +TM −streams −slope | 37.16 | 0.12 | 0.48 | 0.63 | | | | |
| −H50-99yr −PH50-99yr −H≥100yr −P<15yr −PR | | | | | 33.00 | 0.00 | 1.00 | 0.74 |
| Eastern pipistrelle | | | | | | | | |
| +GS +H50-99yr +PH≥100yr +TM +roads +PR +LPI | 75.21 | 0.00 | 0.35 | 0.52 | | | | |
| +GS +H50-99yr +PH≥100yr +TM +roads | 75.91 | 0.69 | 0.25 | 0.45 | | | | |
| +GS +H50-99yr +PH≥100yr +TM +roads +PSCOV | 75.97 | 0.76 | 0.24 | 0.48 | | | | |
| +GS +PH≥100yr −P15-29yr | 76.84 | 1.62 | 0.16 | 0.39 | | | | |
| −PH50-99yr −TM −P15-29yr +LPI +IJI +H100 +roads +P<15yr | | | | | 81.26 | 0.00 | 0.33 | 0.47 |
| −PH50-99yr −TM −P15-29yr +LPI +IJI +H100 +roads | | | | | 81.75 | 0.49 | 0.26 | 0.44 |
| −PH50-99yr −TM −P15-29yr +LPI +IJI +H100 | | | | | 81.82 | 0.56 | 0.25 | 0.41 |
| −PH50-99yr −TM −P15-29yr +LPI +IJI | | | | | 82.83 | 1.57 | 0.15 | 0.37 |

[a] $w_i$ = wt based solely on competing models within 2 units of AIC$_{\mathrm{min}}$.

[b] Sign (+, −) of parameter estimate included in model (effect on probability of roost location); P = pine, H = hardwood, PH = mixed pine and hardwood; GS = group selection, TM = thinned mature, TP = thinned loblolly pine plantations, CP = closed canopy loblolly pine plantations; see Tables 1 and 2 for descriptions of variables and abbreviations for patch configuration metrics.

[c] For distance to roads (roads) and streams (streams), + indicates roosts were more likely further from the feature, and – indicates roosts were more likely closer to the feature than random.