Macrohabitat factors affect day roost selection by eastern red bats and eastern pipistrelles in the southern Appalachian Mountains, USA

Joy M. O'Keefe [a,*], Susan C. Loeb [b], J. Drew Lanham [a], Hoke S. Hill Jr.[c]

[a] Department of Forestry and Natural Resources, Clemson University, Clemson, SC 29634, USA
[b] USDA Forest Service, Southern Research Station, Clemson University, Clemson, SC 29634, USA
[c] Department of Applied Economics and Statistics, Clemson University, Clemson, SC 29634, USA

ABSTRACT

Although roost sites are critically important to bats, we have few data on macrohabitat factors that affect roost selection by foliage-roosting bats. Such data are needed so that forest managers can make informed decisions regarding conservation of bat roosts. Our objective was to examine roost selection by non-reproductive eastern pipistrelles (*Perimyotis subflavus*) and red bats (*Lasiurus borealis*) in a dense deciduous forest undergoing low-intensity timber management in the southern Appalachian Mountains of western North Carolina, USA. During May to August 2004–2006, we radiotracked eight red bats and seven pipistrelles to roosts for 1–14 days (red bats, $\bar{x} = 4.11$ days, $n = 19$ roosts; pipistrelles, $\bar{x} = 7$ days, $n = 15$ roosts). We compared roost and random trees or points using paired-sample t-tests for tree and microhabitat characters and logistic regression models of one to three variables for macrohabitat characters. Neither red bats nor pipistrelles selected roosts based on tree or microhabitat characteristics. Red bats used a wide range of stand ages and conditions and, based on our most plausible models for macrohabitat variables, roosted closer than expected ($\bar{x} = 70.6$ m) to linear openings such as gated roads. Pipistrelles only used stands ≥ 72 years in age and roosted closer than expected ($\bar{x} = 185.6$ m) to non-linear openings and at elevations lower than expected ($\bar{x} = 882$ m). Combined evidence of multiple variables indicated that pipistrelles preferred to roost close to streams. Our results indicate that land managers in the southern Appalachians should maintain a diversity of age classes to provide roosting habitat for both species, and that pipistrelles in particular may benefit from retention of mature stands or buffer zones near perennial streams. Furthermore, non-reproductive red bats and pipistrelles may prefer to roost near openings to minimize commuting costs when openings comprise a small proportion of a densely forested landscape.

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1. Introduction

Bats spend about 15 h per day roosting, so diurnal roost habitat selection is an important component of bat ecology (Barclay and Kurta, 2007). Most roost ecology studies of cavity or crevice-roosting bats have focused on characteristics of the roost tree (e.g., size, decay stage) and its immediate surroundings (e.g., abundance of suitable roosts, canopy closure; Hayes, 2003; Miller et al., 2003; Kalcounis-Rüppell et al., 2005) and significant findings have often been attributed to selection for microclimate characteristics and predator avoidance (Kunz and Lumsden, 2003). In contrast to cavity-roosting bats, foliage-roosting bats in North America are not well-studied and microhabitat and stand-scale factors important in selection of foliage roosts are just beginning to be identified

(Carter and Menzel, 2007). For example, recent studies have found that foliage-roosting bats select roosts based on microhabitat characters associated with suitable microclimate (Willis and Brigham, 2005) or concealment from predators (Perry and Thill, 2007). However, effective conservation of roosting habitat also requires an understanding of how foliage-roosting bats select roosts at macrohabitat (stand and landscape) scales as forest management is generally conducted at these scales.

Eastern red bats (*Lasiurus borealis*) are distributed across much of North America, through Mexico, and deep into South America (Shump and Shump, 1982). Summer roosting ecology of red bats has recently been documented in several regions of North America, though their habit of roosting in foliage has long been known (e.g., Constantine, 1966). Both male and female red bats typically select large-diameter live hardwood trees, particularly hickory (*Carya*), oak (*Quercus*), and gum (*Nyssa* and *Liquidambar*), as day roosts (Menzel et al., 1998; Hutchinson and Lacki, 2000; Mager and Nelson, 2001; Elmore et al., 2004; Leput, 2004; Limpert et al., 2007; Perry et al., 2007) and use stands dominated by large overstory

hardwoods even when pine (*Pinus*) or mixed pine-hardwood stands are readily available (Menzel et al., 1998; Hutchinson and Lacki, 2000; Leput, 2004; Perry et al., 2007; but see Elmore et al., 2004). Adult males and females have very similar roosting habits at the tree, plot, and stand scales in managed mixed pine-hardwood forests in Arkansas, USA (Perry et al., 2007). However, in an intensively managed pine plantation in Mississippi, USA adult females and solitary juveniles roost in thinned pine plantations, whereas adult males favor mature streamside management zones with pines and hardwoods ≥80 years old (Elmore et al., 2004). This same study found little evidence for landscape-scale selection, possibly due to the homogeneity of the landscape in which the study was conducted. However, in park and preserve land on the eastern shore of Maryland, USA, red bats choose sites surrounded by more open urban land and water than random sites (Limpert et al., 2007), possibly because these areas are favored for foraging or commuting (Elmore et al., 2005; Menzel et al., 2005). Red bats in Arkansas roost in areas of low patch diversity and closer to roads at the site specific scale and in areas dominated by larger patches with lower amounts of seed-tree harvesting at a landscape scale (Perry et al., 2008).

Eastern pipistrelles (*Perimyotis subflavus*) are common in eastern North America (Fujita and Kunz, 1984) and roost in clusters of live or dead leaves in mature hardwood trees, typically oaks (Veilleux et al., 2003; Leput, 2004; Perry and Thill, 2007) or in dead needles in live shortleaf pine (*P. echinata*; Perry and Thill, 2007). In Indiana, USA, pipistrelles select riparian and upland forests over bottomland forests (Veilleux et al., 2003) and, in South Carolina, USA roost closer to water than expected (Leput, 2004), which may relate to their preference for foraging in riparian habitats (Ford et al., 2005; Menzel et al., 2005). In Arkansas, both sexes display stand-scale preferences for roosts in mature stands or stream buffers within recently or partially harvested stands (Perry and Thill, 2007) and landscape-scale preferences for areas with a diversity of patch types and sizes that are farther from roads than random (Perry et al., 2008). In an intensively managed pine landscape in Mississippi, eastern pipistrelles roost exclusively in mature (>80 years old) hardwoods in riparian buffers (D.A. Miller, Weyerhaeuser Company, personal communication).

There are still relatively few data on the macrohabitat factors that affect roost selection by eastern red bats and eastern pipistrelles and more information is needed to enable forest managers to make informed decisions regarding conservation of bat roosts. We examined roosting ecology of these two bat species in a dense temperate deciduous forest subjected to low-intensity timber management in the southern Appalachian Mountains, North Carolina, USA. Our objectives were to describe characteristics of day roosts for non-reproductive bats and examine roost selection at the tree, microhabitat, stand and landscape scales. Thermal properties of roosts may be less important for male and non-reproductive female bats than for pregnant and lactating bats (Kunz and Lumsden, 2003) and, thus, non-reproductive bats may display macrohabitat preferences for roost sites that enable them to minimize energy costs associated with commutes to foraging sites (Broders et al., 2006; Hein et al., 2008). Therefore, we predicted that foraging ecology would influence roost selection such that red bats would roost closer to open areas and pipistrelles would roost closer to streams.

2. Methods

2.1. Study area

We conducted our study from May to August 2004–2006 on the Wayah Ranger District of the Nantahala National Forest in Macon County, North Carolina. Our study site was Trimont Ridge, a 2300-ha tract (83°29′E, 35°11′N) that ranged in elevation from 700 to 1200 m. The study area was >99% USDA Forest Service property (USFS), with small inholdings of private land. Oaks, tulip poplar (*Liriodendron tulipifera*), and hickories were the most common overstory hardwoods while white pine (*P. strobus*) was the most common overstory conifer. Most of the area (>83%) was dominated by upland hardwood (oak-hickory, 1235 ha) and cove hardwood forest types (poplar-oak, 890 ha), with fewer mixed pine-hardwood stands (15%; 192 ha) or white pine stands (1%; 22 ha). Based on stand ages in 2005, 124 ha (5.4%) of the area was early successional (≤15 years), 314 ha (13.7%) was sapling/pole (16–39 years), 673 ha (29.3%) was mid-successional (40–79 years), and 1232 ha (53.6%) was late successional (≥80 years). However, during October 2005–December 2006, three stands (25 ha) were harvested via 2-age cuts.

The study area was dissected by approximately 62 km of roads, 75% of which were gated grass-covered USFS roads that received virtually no vehicular traffic. We classified two well-maintained ridgetop hiking trails as small linear openings. Wildlife openings (*n* = 57, 31 ha total, 0.01–3.12 ha each) maintained in grasses by annual mowing and 43 ha of 2-age cut stands ≤5 years in age (3.12–10.95 ha) were the only nonlinear openings. Over 35 km of perennial streams (typically 2–3 m wide) drained our site, fed by numerous smaller intermittent streams (typically 1–2 m wide).

Mean minimum and maximum daily temperatures from 1 May to 31 August were 16.1 and 27.3 °C in 2004, 16.8 and 28.0 °C in 2005, and 15.3 and 27.8 °C in 2006. Precipitation in the same period was 32.5 cm in 2004, 45.0 cm in 2005, and 23.1 cm in 2006. Temperature and precipitation data were measured at the Macon County Airport, ~8 km east of the study area center (State Climate Office of North Carolina).

2.2. Sampling

We conducted mist net surveys on 55 nights at 17 sites. At each site, we deployed 1–3 "net sets" consisting of two stacked 6–12 m mist nets (Avinet, Inc., Dryden, NY) set over road corridors within USFS property boundaries or beside a small pond <25 m from the USFS boundary. We opened nets at sunset and monitored them at 10 min intervals for 3–4 h. We identified captured bats to species and determined sex, age, forearm length (mm), and weight (g), and banded each with a unique aluminum forearm band (USFS-SRS or USFS-NC; Lambournes, Ltd., Birmingham, UK). We trimmed fur and used surgical glue (Torbot Group, Inc., Cranston, Rhode Island, USA) to attach a 0.35 g (pipistrelles) or 0.42–0.52 g (red bats) radio-transmitter (Holohil Systems, Ltd., Ontario, Canada) between the scapulae. We held bats until the glue dried and released them at the point of capture. Radio transmitters were 5.6–6.6% of body weight for pipistrelles and 3.8–5.1% of body weight for red bats. Animal capture and handling methods were approved by the Clemson University Animal Research Committee (Animal Use Protocol 40065).

We used a 3-element Yagi antenna and a TR5 (Telonics, Inc., Mesa, Arizona, USA) or R1000 (Communication Specialists, Inc., Orange, California, USA) receiver to locate bats at day roosts. We radiotracked bats until the radiotransmitter failed (signal weakened) or fell off, or until the bat left the study area (usually ≤1 week). We located roosts by homing in on the signal and triangulating around the point where the signal was strongest prior to designating a tree as the roost. When we could not confirm the roost through visual sightings of bats or emergence observations, we used the suspected tree as the bat's location. For each roost tree or location, we identified a corresponding random tree 50 m away in a random direction.

2.3. Roost tree and microhabitat characteristics

We recorded species, diameter at breast height (dbh; cm), and height (m) of each roost tree and corresponding random tree and species and dbh for all live and dead trees >10 cm dbh within 11.3 m (0.04 ha) of the roost and random trees. We used diameter measurements to calculate plot basal areas for live and dead trees. We measured distance to and height of the closest tree ≥10 cm dbh to roost and random trees, and closest tree the same height or taller than roost and random trees. We counted all saplings (single woody stems <10 cm dbh and ≥2 m in height) along 2-m-wide transects extending 11.3 m away from roost and random trees in the four cardinal directions. For each quarter plot, we visually estimated percent canopy closure to nearest 25%. Sapling counts and canopy closure estimates were averaged for each plot.

2.4. Stand and landscape-scale data

We used a geographic information system (GIS; ArcView 3.2 and ArcGIS 9.2; ESRI, Redlands, California) with data from the USFS Continuous Inventory of Stand Conditions (CISC) to examine habitat conditions relative to bat roost and random locations. We also used road and wildlife opening layers from the USFS and converted road shapefiles to polygons by applying a 3 m buffer (total width of 6 m). We obtained spatial data on trails from the Southern Appalachian Assessment GIS Online Database (http://www.samab.org/data/SAA_data.html) and converted these to polygons by applying a 0.75 m buffer (total width of 1.5 m). From these, we created a polygon layer of linear openings by combining road and trail polygons and a nonlinear opening layer by merging wildlife openings and USFS stands ≤5 years in age. We used a comprehensive stream layer that was generated by the North Carolina Stream Mapping Program (NC Center for Geographic Information and Analysis, http://www.ncstreams.org) using light detection and ranging (LiDAR) data and digital aerial imagery. We separated streams into two layers; we used topographic maps to identify perennial streams and classified all other streams as intermittent.

We used a Recon GPS unit (Trimble Navigation Ltd., Sunnyvale, California) to determine coordinates of each roost location and all capture sites. We plotted points in the GIS, calculated the maximum distance traveled between two successive locations for each bat, and then determined mean maximum travel distance for each species. To identify available habitat types within the range of roosting bats, we defined a study area by creating a 100% minimum convex polygon (MCP) for each species using all roost locations and buffering this with

mean maximum travel distance moved by that species (Miles et al., 2006). Within the boundary of the buffered MCP, we generated a random point for every roost location, replacing any random points that fell on non-USFS property. Each point was buffered with the mean maximum travel distance and within that buffer we calculated area of linear and nonlinear openings and total length of perennial and intermittent streams. We also calculated distance to the closest intermittent stream, perennial stream, linear opening (road or trail), and nonlinear opening for each roost and random point. We determined forest type and stand age (in 2005) using CISC data and elevation using a 10 m resolution US Geological Survey digital elevation model for Macon County (http://216.119.24.38/website/macgis). We did not use forest type in the statistical analysis because all but three roosts and two random points were in upland or cove hardwood forests. These two forest types are best differentiated by their proximity to streams. We also calculated roosting range (100% MCP) for bats that used ≥3 roosts.

2.5. Statistical analyses

Due to a low sample of radiotagged bats, we used roosts rather than bats as the experimental unit and assumed observations were independent. For the same reason, we pooled roost data across years and did not test for temporal variation in roost selection. We used SAS® (SAS Institute Inc., 2004) to conduct all statistical analyses outlined below.

For tree and microhabitat data, we tested 12 independent variables (Table 1) for normality using the Shapiro-Wilk W statistic. For normally distributed data, we compared roost and random data using two-tailed paired-sample t-tests. We transformed non-normal data using logarithm or square root transformations and tested the transformed data for normality using the Shapiro-Wilk W statistic. If data were normal after transformation, we used two-tailed paired-sample t-tests to compare transformed data for roost and random sites. Otherwise, we used Wilcoxon signed rank tests to compare untransformed data. We report untransformed means ± 1 standard error.

For stand and landscape-scale variables (Table 2), we constructed a global logistic regression model for each bat species with use (roost or random) as the dependent variable to test for multicollinearity. Because variance inflation factors were ≤5.3 in all tests, we determined that multicollinearity was not a problem and used all 10 variables in subsequent analyses for each species. We constructed logistic regression models, with use as the dependent variable, for each bat species. Because our sample of roost trees was small, we only examined candidate models with one to three variables (Psyllakis and Brigham, 2006). Because little

Table 1
Mean, standard error (S.E.), minimum (min), and max (maximum) values for tree and microhabitat variables for roosts used by eastern red bats and eastern pipistrelles in southwestern North Carolina, 2004–2006. Tree and microhabitat characteristics did not differ from random points for either bat species ($P \geq 0.32$).

Variable	Red bats				Eastern pipistrelles			
	Mean	S.E.	Min	Max	Mean	S.E.	Min	Max
Roost tree height (m)	16.9	3.0	4.0	37.4	26.9	4.9	15.0	54.0
Dbh (cm)	28.3	6.1	3.0	80.0	26.5	4.3	13.6	46.5
Distance to nearest tree (m)	2.9	0.1	0.5	7.0	1.5	0.3	0.5	3.0
Height of nearest tree (m)	17.2	2.4	5.0	29.5	19.7	4.2	3.4	43.5
Distance to nearest taller tree (m)	5.8	1.7	0.5	18.0	4.6	0.9	2.0	8.0
Height of nearest taller tree (m)	19.1	2.5	5.0	29.5	27.8	4.6	10.0	43.5
Saplings (0.2 ha)	951.3	115.0	150.0	1825.0	662.5	132.6	200.0	1650.0
Canopy closure (%)	63.5	4.6	12.5	100.0	58.1	7.4	25.0	76.3
Live tree basal area (m²/ha)	16.9	1.6	3.6	28.6	25.6	3.7	0.4	45.8
Live trees (ha)	426.4	44.0	75.0	750.0	377.08	43.6	50.0	625.0
Dead tree basal area (m²/ha)	1.6	0.6	0.0	8.8	1.6	0.8	0.0	8.5
Dead trees (ha)	33.3	7.6	0.0	100.0	37.5	14.3	0.0	125.0

Table 2

Stand and landscape variables used in candidate models of roost selection by eastern red bats and eastern pipistrelles in southwestern North Carolina, 2004–2006.

Variable	Units	Definition
age	years	Stand age in 2005
elevation	m	Digital elevation in 10 m grid cell containing point
dist_linopen	m	Distance to linear opening (road/trail)
dist_nonlinopen	m	Distance to non-linear opening (cut/wildlife opening)
dist_perstrm	m	Distance to perennial stream
dist_intstrm	m	Distance to intermittent stream
den_linopen	ha/ha	Density of linear openings inside buffer[a]
den_nonlinopen	ha/ha	Density of non-linear openings inside buffer
den_perstrm	m/ha	Density of perennial streams inside buffer
den_intstrm	m/ha	Density of intermittent streams inside buffer

[a] Buffer radius is 450 m for red bats and 600 m for pipistrelles.

is known about stand and landscape-scale selection for either species, we explored a large set (175) of candidate models. We used Akaike's information theoretic procedures to rank models by their respective Akaike's information criterion for small sample sizes (AIC$_c$) and computed Akaike weights (w_i) to compare plausibility of competing models (Burnham and Anderson, 2002). We considered the model with the lowest value for AIC$_c$ to be the best model, and models with ΔAIC$_c \leq 2$ to be plausible. Variables in these models were considered important in discriminating between roost and random sites. We averaged parameter estimates for important variables using values from the candidate model with the highest w_i and all subsequent models in which those variables appeared until the sum of the weights (Σw_i) for the model set was equal to 0.95 (Burnham and Anderson, 2002). For variables in plausible models, we present adjusted odds ratios and unconditional standard errors calculated from averaged parameter estimates. To aid in model interpretation we used plots to explore relationships between use (roost or random) and each of the independent variables.

3. Results

We captured 168 big brown bats (*Eptesicus fuscus*), 48 eastern red bats, 7 eastern small-footed bats (*Myotis leibii*), 4 little brown bats (*M. lucifugus*), 82 northern long-eared bats (*M. septentrionalis*), and 16 eastern pipistrelles. Four red bats were non-reproductive females captured 30 July or later and the rest were males; all captured pipistrelles were male. We placed radiotransmitters on 12 eastern red bats (9 adult males, 2 juvenile males, and 1 juvenile female) and located 18 roosts for seven adult males and one roost for a juvenile female. We placed radiotransmitters on eight male eastern pipistrelles (seven adult and one juvenile) but one adult was never relocated. Red bats were tracked for 4.1 ± 1.2 days (range 1–10), used 2.2 ± 0.7 (range 1–6) trees each, and remained in trees for 1.7 ± 0.32 (range 1–6) days. Pipistrelles were tracked for 7 ± 1.5 (range 1–14) days, used 2.3 ± 0.5 (range 1–4) trees each, and remained in trees for 2.5 ± 0.5 (range 1–6) days. Three red bats and two pipistrelles returned to a previously used tree after roosting in a different tree.

We calculated roosting range for three red bats: one used three roosts in 0.01 ha in 10 days; one used five roosts in 1.5 ha in 13 days; and another used six roosts in 9.14 ha in 6 days. Mean maximum distance among locations for all red bats was 450 ± 91 m (range 2.1–836.5 m). We also calculated roosting range for three male pipistrelles: one used three roosts in 0.02 ha in 10 days; one used three roosts in 0.08 ha in 14 days; and a third used three roosts in 3.19 ha in 6 days. Mean maximum distance among locations for all pipistrelles was 600 ± 225 m (range 14.3–1817.9 m).

3.1. Roost tree and microhabitat characteristics

We tracked red bats to hickories ($n = 5$), oaks ($n = 4$), poplars ($n = 3$), sassafras (*Sassafras albidum*; $n = 2$), an American chestnut (*Castanea dentata*), a birch (*Betula*), a maple (*Acer*), a rhododendron (*Rhododendron*), and a sourwood (*Oxydendrum arboreum*). With respect to micro- and macrohabitat characteristics, the single roost we located for the juvenile female was similar to roosts used by multiple male red bats in this study. We visually confirmed four roosts close to the ground for three males: one roosted for 2 days 1.5 m above ground in dried dead leaves in a downed 25.9 cm dbh scarlet oak (*Q. coccinea*); one spent 1 day 6 m high in a 10.6 cm dbh sourwood in an early successional stand; and one bat roosted 2 m above ground in a 3 cm dbh sassafras for 4 days and 6 m high in a 7.3 cm dbh American chestnut for 3 days (we do not know if bats left these roosts at night or if they roosted continuously). Based on radio signals, we suspected all other red bat roosts were high ($\geq$10 m) above ground.

Male pipistrelles were tracked to hickory ($n = 4$), maple ($n = 2$), birch ($n = 2$), a poplar, an oak, a Fraser magnolia (*Magnolia fraseri*), and a white pine. Though we never visually confirmed any of these roosts, we suspected the pipistrelle using the white pine was hidden in a cluster of dead leaves caught in the branches of the pine ~25 m high. Radiotelemetry signals always indicated foliage roosting in live trees (i.e., no evidence to suggest pipistrelles were roosting in cavities of dead or damaged trees).

Tree and microhabitat characteristics did not differ significantly ($P \geq 0.32$) between red bat roost and random sites (Table 1). Red bats used large diameter trees of moderate height similar to surrounding tree heights. Ten red bat roosts were in stands with 450–750 live trees/ha and nine roosts were in stands with 1025–1825 saplings/0.2 ha. Tree and microhabitat characteristics also did not differ ($P \geq 0.47$) between male pipistrelle roosts and corresponding random sites (Table 1). Pipistrelles used tall, large diameter trees that were taller than the nearest tree but not necessarily the tallest tree in the plot.

3.2. Stand and landscape selection

Nine red bat roosts were in cove hardwood (poplar-oak) stands and 10 were in upland hardwood stands (7 in oak-hickory, 2 in oak-pine, and 1 in white pine-upland hardwood). Both plausible models for red bat roost selection contained distance to linear openings and elevation (Table 3). Only distance to linear openings had a relative-importance weight >0.60 and confidence intervals that did not contain 0 (Table 4). Red bats roosted closer to linear openings than expected and for every 50 m decrease in distance to linear opening, odds that a red bat would use a site increased 1.77 times (95% CI: 0.67–4.69). Plausible models showed that red bats selected sites at lower elevations, with a greater length of perennial streams, but farther from intermittent streams (Tables 4 and 5). Distance to permanent streams was not an important predictor of use (Table 4). Although mean distance to nonlinear openings was two times greater for random sites than for red bat roost sites (Table 5), the random site mean was strongly influenced by two points >900 m from a nonlinear opening and distance to nonlinear openings did not appear in plausible models.

Three male pipistrelle roosts were in upland hardwood (oak-hickory) stands and 12 were in cove hardwood (poplar-oak) stands. Distance to nonlinear opening was in every plausible macrohabitat model for pipistrelles and elevation was in all but one plausible model (Table 3). Both distance to nonlinear opening and elevation had relative-importance weights >0.60 but only distance to nonlinear opening had a confidence interval that did not contain 0 (Table 4). For every 50 m decrease in distance to nonlinear opening, chances that a pipistrelle would use the site

Table 3

Akaike's information criterion for small sample sizes (AIC$_c$), difference in AIC$_c$ value when compared to the model with the lowest AIC$_c$ value (ΔAIC$_c$), and Akaike weight (w_i) for models with ΔAIC$_c$ ≤ 2 from the a priori set of 175 candidate models used to predict stand and landscape level roost-site selection by eastern red bats and eastern pipistrelles in southwestern North Carolina, 2004–2006.

Model[a]	AIC$_c$	ΔAIC$_c$	w_i
Red bats			
dist_linopen elevation dist_intstrm	40.578	0.000	0.1698
dist_linopen elevation den_perstrm	41.962	1.384	0.0850
Eastern pipistrelles			
dist_nonlinopen den_intstrm elevation	21.349	0.000	0.1344
dist_nonlinopen den_intstrm den_nonlinopen	21.930	0.581	0.1005
dist_nonlinopen elevation age	22.401	1.052	0.0794
dist_nonlinopen elevation	22.566	1.217	0.0731
dist_nonlinopen elevation dist_intstrm	22.795	1.446	0.0652
dist_nonlinopen elevation den_nonlinopen	22.797	1.448	0.0651
dist_nonlinopen elevation den_intstrm	22.822	1.473	0.0643
dist_nonlinopen elevation dist_perstrm	23.306	1.957	0.0505

[a] Refer to Table 2 for variable definitions.

Table 4

Model averaged parameter estimates, unconditional standard errors (S.E.s), odds ratios, and sum of Akaike weights (Σw_i) of predictor variables found in plausible models (ΔAIC$_c$ ≤ 2) for eastern red bat and eastern pipistrelle roost selection in southwestern North Carolina, 2004–2006.

Bat species and parameter[a]	Estimate	S.E.	Odds ratio	Σw_i
Red bats				
dist_linopen	−0.0114	0.0099	0.9886	0.6824
elevation	−0.0104	0.0140	0.9897	0.4977
den_perstrm	0.0504	0.0735	1.0517	0.3466
dist_intstrm	0.0052	0.0090	1.0052	0.2359
Eastern pipistrelles				
dist_nonlinopen	−0.0203	0.0123	0.9800	0.9938
elevation	−0.0139	0.0145	0.9862	0.6140
den_intstrm	0.1362	0.2182	1.1459	0.3261
den_nonlinopen	−27.2482	46.8322	0.0000	0.2413
dist_intstrm	−0.0112	0.0195	0.9889	0.2216
dist_perstrm	−0.0036	0.0065	0.9964	0.1866
age	0.0076	0.0176	1.0077	0.0949

[a] Refer to Table 2 for variable definitions.

increased by 2.75 (95% CI: 0.82–9.19). Chances that a pipistrelle would use a site increased two times (95% CI: 0.48–8.33) for every 50 m decrease in elevation. Although individual weights for stream-related parameter estimates were low (Table 4), six plausible models included some measure of proximity to, or length of, streams (Table 3). On average, male pipistrelles roosted 36 m from intermittent streams (never >105 m), 96 m from perennial streams (never >280 m) and in areas with 46 m of intermittent streams in the surrounding buffer (Table 6). Stand age appeared in one plausible model (Table 3), and the positive parameter estimate (Table 4) indicated that male pipistrelles selected more mature stands. Random sites were in 17- to 127-

year-old stands while pipistrelles used stands 72–114 years old (Table 6). One bat roosted in a stand that was being cleared but in our analysis we used the stand age prior to harvest. The negative parameter estimate for density of nonlinear openings (Table 4) indicated that male pipistrelles avoided sites with a higher relative area of nonlinear openings in the surrounding buffer. However, nonlinear openings comprised 5.5–9.2% of the 600 m buffer for 6 pipistrelle roosts, but never comprised >5.6% of the 600 m buffer for random points (Table 6). Furthermore, there were 2.3 ± 0.1 (1–4) openings around pipistrelle roosts, averaging 1.3 ± 0.1 (0.09–3.38) ha each and 1.7 ± 0.1 (0–6) openings around random points, averaging 0.9 ± 0.1 (0.0–5.86) ha each.

Table 5

Mean, standard error (S.E.), minimum (min), and maximum (max) values of stand and landscape variables measured for eastern red bat roosts and associated random sites in southwestern North Carolina, 2004–2006.

Variable[a]	Roost				Random			
	Mean	S.E.	Min	Max	Mean	S.E.	Min	Max
stand age (years)	73.53	9.98	5.00	127.00	73.84	8.60	18.00	127.00
elevation (m)	926.43	13.59	846.44	1020.32	957.49	19.96	787.19	1114.06
dist_linopen (m)	70.58	18.08	10.00	302.55	150.93	30.50	7.71	406.84
dist_nonlinopen (m)	157.82	31.36	0.00	407.00	348.91	57.96	69.69	974.64
dist_perstrm (m)	261.94	35.00	15.85	527.83	311.72	36.37	58.11	553.09
dist_intstrm (m)	71.55	12.04	3.70	203.28	62.95	12.18	9.27	219.74
den_linopen (%)	1.58	0.11	0.98	2.61	1.46	0.20	0.09	3.18
den_nonlinopen (%)	1.98	0.94	0.00	15.16	2.82	0.73	0.00	9.74
den_perstrm (m/ha)	11.22	1.53	0.00	21.26	7.61	1.81	0.00	27.67
den_intstrm (m/ha)	37.52	2.65	24.05	72.30	40.00	2.05	23.48	57.40

[a] Refer to Table 2 for variable definitions.

Table 6

Mean, standard error, minimum and maximum values of stand and landscape variables measured for eastern pipistrelle roosts and associated random sites in southwestern North Carolina, 2004–2006.

Variable[a]	Roost				Random			
	Mean	S.E.	Min	Max	Mean	S.E.	Min	Max
stand age (years)	79.40	2.60	72.00	114.00	81.53	7.69	17.00	127.00
elevation (m)	882.02	25.08	797.48	1145.40	992.54	28.92	830.82	1223.30
dist_linopen (m)	136.54	25.17	4.00	285.20	189.27	37.97	13.53	546.39
dist_nonlinopen (m)	185.58	35.78	0.00	369.31	395.43	40.47	31.80	640.30
dist_perstrm (m)	95.79	21.58	5.73	279.39	227.09	34.29	14.75	572.52
dist_intstrm (m)	35.59	7.25	4.97	104.33	88.47	14.01	18.52	196.49
den_linopen (%)	1.39	0.07	0.84	1.67	1.25	0.15	0.12	2.06
den_nonlinopen (%)	3.10	0.98	0.13	9.24	1.33	0.51	0.00	5.58
den_perstrm (m/ha)	13.32	1.53	4.34	21.54	10.33	1.65	0.57	20.68
den_intstrm (m/ha)	45.85	2.44	35.72	63.09	38.68	1.60	30.24	50.82

[a] Refer to Table 2 for variable definitions.

4. Discussion

We found that tree, microhabitat, and stand-scale traits were not significant factors in roost-site selection by non-reproductive eastern red bats and male eastern pipistrelles. However, we found that both species selected roosts based on proximity to particular landscape features. The lack of significance for microhabitat traits contrasts with some studies on roost selection for red bats and pipistrelles (e.g., Hutchinson and Lacki, 2000; Veilleux et al., 2003; Elmore et al., 2004; Perry and Thill, 2007). The disparity between our study and other studies may have been due to the relative uniformity of microhabitat conditions across our study area. However, landscape factors may also have been more important in our study because we focused on non-reproductive individuals which may select roosts at the macrohabitat scale to minimize commuting costs [e.g. red bats, Elmore et al., 2004 and Seminole bats (*Lasiurus seminolus*), Hein et al., 2008] as opposed to reproductive females which may select roosts at the microhabitat scale to minimize thermoregulatory costs.

As we predicted, red bats roosted closer to open areas, particularly linear openings that probably served as commuting corridors. Proximity to nonlinear openings was an important factor in roost selection for male pipistrelles, and we found support for our prediction that pipistrelles would choose roost sites close to streams. Proximity to foraging habitat (openings or streams) may be particularly important for pipistrelles as they are smaller and not as well-adapted for long-distance flight as red bats (Norberg and Rayner, 1987). Although we found evidence that pipistrelles commuted long distances to use a pond, we doubt that pipistrelles prefer to make such long commutes and we have limited evidence that male pipistrelles have small roosting ranges.

Red bats primarily used the three most common genera of large overstory hardwoods (oaks, hickories, and poplars) and the two most common hardwood forest types available in our study area. In general, red bats prefer to roost in hardwood trees, even in landscapes in which pines are abundant (Menzel et al., 1998; Hutchinson and Lacki, 2000; Elmore et al., 2004; Leput, 2004; Perry et al., 2007). Consistent with previous studies (e.g., Menzel et al., 1998; Mager and Nelson, 2001; Perry et al., 2007) red bats we radiotracked used primarily large diameter hardwoods, but we also visually confirmed that red bats used small diameter trees and saplings as was found in Mississippi (Elmore et al., 2004).

Stand age was not a significant factor in red bat roost selection. Some studies (e.g., Hutchinson and Lacki, 2000; Limpert et al., 2007; Perry et al., 2007) have shown that red bats prefer mature stands, possibly because of preferences for roosting in mature hardwood trees. However, non-reproductive red bats in our study occasionally roosted in early successional or sapling/pole stands even though stands ≥80 years old were widely available in the area. The wide range of stand ages and conditions used by red bats in our study, in Mississippi (Elmore et al., 2004), and in Arkansas (Perry et al., 2007) suggest that, with respect to roost habitat selection, non-reproductive red bats are tolerant of timber harvesting (but see Hutchinson and Lacki, 2000). Furthermore, red bats roosted closer than expected to linear openings, suggesting that roads built for timber harvest operations may be used by red bats for commuting and/or foraging. Perry et al. (2008) also found that red bat roosts were closer to roads than random sites. In contrast, Hutchinson and Lacki (2000) never found red bat roosts <50 m from edge habitat and suggested that, in unfragmented forests, red bats might avoid roosting near edges to minimize predation risk. Although we did not measure distance to all types of edges, we found that on average red bats roosted 71 and 158 m from linear and nonlinear openings, respectively, and like Perry et al. (2007, 2008) found that red bats will roost near edges. Red bats primarily forage in open habitats (Mager and Nelson,

2001; Menzel et al., 2002; Loeb and O'Keefe, 2006), which may be necessitated by their relatively high wing loading (Lacki et al., 2007). Although roosting near edges may increase predation risk, non-reproductive red bats may prefer to trade increased risk for decreased commuting costs.

Male eastern pipistrelles primarily roosted in hickories, maples, and birches. Only one roost was thought to be in an oak, which was surprising because pipistrelles select oaks over other species in Indiana, South Carolina, and Arkansas (Veilleux et al., 2003; Leput, 2004; Perry and Thill, 2007). However, because our sample size was small, we do not have sufficient evidence to say that pipistrelles used oaks less than expected. Like Perry and Thill (2007), we found that pipistrelles used conifers, but probably only when there is dead vegetation that provides concealment.

Although stand age was not an important predictor of male pipistrelle roost-site selection, pipistrelles only used stands ≥72 years old. Previous studies (Veilleux et al., 2003; Leput, 2004; Perry and Thill, 2007) showed that pipistrelles select mature hardwood stands with an open understory. We found no evidence for stand-scale selection, which was not surprising in a landscape dominated by mature hardwood stands. However, canopy closure values for this study (58%) and other studies (41–70%; Veilleux et al., 2003; Leput, 2004; Perry and Thill, 2007) are not characteristic of a closed canopy and indicate that pipistrelles may use portions of mature stands where there is more light due to a canopy gap or an edge.

Several landscape characteristics were important in male pipistrelle roost selection. When compared to random sites, pipistrelles roosts were closer to nonlinear openings ($\bar{x} = 186$ m) and often in areas with more openings in the surrounding buffer. We suspect that in our study area the optimal distance to an edge is ≥100 m because despite the fact that pipistrelles roosted closer to edges than expected, they roosted farther from edges than in previous studies (52 and 70 m, Veilleux et al., 2003 and Leput, 2004; respectively). Because pipistrelles are commonly recorded foraging in early successional habitats (Ellis et al., 2002; Loeb and O'Keefe, 2006) they may roost closer to openings to minimize commuting costs.

Although model averaged weights for length of intermittent streams, distance to intermittent stream, and distance to perennial stream were low (Table 4), their inclusion in the top models combined with pipistrelles' preference for low elevation sites suggest that proximity to streams is an important factor in roost-site selection by male pipistrelles. Furthermore, 12 of 15 pipistrelle roosts were in cove hardwood forests which are associated with streams. Others have also found that pipistrelles favor riparian habitats, whether for foraging (Owen et al., 2004; Ford et al., 2005; Menzel et al., 2005) or for the mature hardwood trees retained in riparian areas on landscapes with timber harvest (Perry and Thill, 2007). In Arkansas, pipistrelles select stands with a mature hardwood component (Perry et al., 2008) but mature hardwoods were not restricted to riparian zones at our study site and thus, it is possible that in our study area pipistrelles roosted near streams to maximize foraging efficiency.

5. Management implications

Non-reproductive red bats in our study sometimes roosted in early successional stands but we recommend maintaining a diversity of age classes within a forest landscape because mature stands may provide benefits, such as low clutter foraging habitat, not identified by our study design. In addition, if maintenance of stand-level habitat quality for red bats is a management objective, we recommend retaining a basal area of ≥3.6 m²/ha of hardwoods >10 cm dbh during timber harvest operations as this was the lowest value for a stand used by a red bat in our study. Because proximity to linear openings was the most important factor in

roost selection in this study, non-reproductive eastern red bats may also benefit from creation of linear, and possibly nonlinear, openings in a densely forested landscape.

Although male pipistrelles never used stands <72 years, male pipistrelles may benefit from creation of small nonlinear openings (<5 ha) in a densely forested area when these openings represent only a minor percentage of the landscape. As a whole, our data suggest that male pipistrelles would favor roost sites in mature stands near streams with small openings nearby. Alternately, they may roost within large (≥100 m) riparian buffer zones adjacent to newly harvested stands when ≥14.5 m²/ha basal area of hardwoods >10 cm dbh are retained in these buffers. Although not tested in our study, our capture data indicate that small ponds could be important foraging areas for pipistrelles as some bats foraged over a small pond 900–1800 m from their roost sites. Because small ponds also function as openings, pipistrelles might use both types of openings equally for their structure or may favor one or the other for prey availability. We recommend that future studies test hypotheses about the role of small (>0.1 ha) openings (whether wet or dry) in roosting and foraging ecology of eastern pipistrelles in mature hardwood-dominated forests where openings and permanent water bodies are sparse or absent.

Acknowledgements

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