TREE ROOSTING BY MALE AND FEMALE EASTERN PIPISTRELLES IN A FORESTED LANDSCAPE

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Little information has been published on selection of tree roosts by eastern pipistrelles (*Perimyotis subflavus*) in forested environments, and no radiotelemetry-based studies have been conducted on males in forested settings. Therefore, we used radiotelemetry to characterize summer roost selection by 21 male (33 roosts) and 7 female (14 roosts) eastern pipistrelles during 6 years in a forested region of the Ouachita Mountains of Arkansas. All roosts were located in the vegetation of tree canopies; 50% of roosts of females and 91% of roosts of males were in dead leaves of deciduous trees. Three (43%) of 7 maternity colonies were in dead needles of large live pines (*Pinus echinata*); this is the 1st documented use of pines by this species for roosting. Males selected tree sizes randomly but females selected trees that were larger ($P < 0.05$) than random. For males, 87% of roosts were in oaks (*Quercus*), and males roosted at sites with more midstory hardwoods, more large pines in the overstory, less canopy cover, and farther from the nearest trees than random locations. In a landscape offering a diversity of forest habitats, eastern pipistrelles during summer roosted mostly in leaves of oaks in mature ($\geq$50-year-old) forest with a relatively complex structure and a hardwood component.

Key words: Arkansas, bats, Interior Highlands, Ouachita Mountains, *Perimyotis*, pipistrelle bat, *Pipistrellus subflavus*, roost selection, roosting

Concern over habitat loss and declining populations of bats has prompted considerable research in the last decade (Kalcounis-Rüppell et al. 2005). For effective conservation, information on the biology and ecology of each species is needed. The eastern pipistrelle (*Perimyotis subflavus*; hereafter, pipistrelle) is a relatively common bat that occurs throughout most of eastern North America and parts of the midwestern United States (Fujita and Kunz 1984). During winter, it hibernates in caves, buildings, and other man-made structures (e.g., Davis 1964; LaVal and LaVal 1980; Mumford and Whitaker 1975; Sandel et al. 2001). During summer, maternity colonies are commonly found in barns, buildings, other man-made structures, and caves (Humphrey 1975; Jones and Pagels 1968; Jones and Suttkus 1973; Lane 1946). Because roosts in caves and man-made structures are conspicuous, historical research has focused on these roosting structures.

Surprisingly little research has been conducted on pipistrelles in forested environments even though the species is commonly captured in these areas (e.g., Miller 2003; Saugey et al. 1989; Wilhide et al. 1998). Until recently, no information was available on use of tree roosts by pipistrelles other than a few anecdotes (Carter et al. 1999; Davis and Mumford 1962; Findley 1954; Kurta et al. 1999; Menzel et al. 1996). In the 1st comprehensive radiotelemetry-based study of summer roosting, Veilleux et al. (2003) found female pipistrelles roosted among dead or live leaves in deciduous tree canopies in a forest–agriculture mosaic in Indiana. However, no studies have investigated selection of summer roosts by males in forested environments.

Roost sites selected by females may differ from those of males during summer because of the added physiological requirements associated with reproduction, lactation, and avoidance of predators when pups are nonvolant. Further, it is unknown if roosting in dead leaves, as observed for females in Indiana and South Carolina (Leput 2004; Veilleux et al. 2003), is a ubiquitous trait across the range of this species. Therefore, we used radiotelemetry to characterize roost selection at the tree, site, and stand level by male and female eastern pipistrelles. We compared attributes of roosts between males and females and compared those roost locations to random trees during summer in a diverse forested landscape of Arkansas. We also compared sites selected by males with random locations and examined forest stands selected by both sexes.

MATERIALS AND METHODS

Study area.—We conducted our study in the 6,545-ha Upper Lake Winona Basin, situated in the Ouachita Mountains of central Arkansas (approximately 34°48′N, 92°58′W). The Ouachita Mountains are a series of east- to west-oriented ridges and valleys with elevations of 152–853 m above mean sea level, mean annual precipitation of 112–137 cm, and mean annual temperatures of 13.9–16.1°C (Skiles 1981).

No residential areas, farms, houses, agricultural lands, or pastures existed within the study portion of the Winona Basin. Although most of the basin consisted of mixed shortleaf pine (*Pinus echinata*)–hardwood forests managed by the United States Forest Service (Ouachita National Forest), the basin also contained a mix of other forest types including oak (*Quercus*)–hickory (*Carya*) and riparian hardwood forests. Twelve percent (778 ha) of the study area was intensively managed industrial timberlands consisting primarily of closed canopy and older thinned plantations of loblolly pine (*Pinus taeda*) that were generally thinned and pruned at about 12–15 years of age.

National Forest lands within the basin were divided into management units where different silvicultural treatments were implemented in 2000 as part of a multidisciplinary research project (Guldin 2004). A 2,096-ha block was partially harvested with retained overstory basal areas of pine at 13.8 m²/ha and hardwood at 1.1–2.3 m²/ha. That block underwent midstory removal whereby most hardwoods < 15 cm diameter at breast height (dbh) were felled. A 1,044-ha area was harvested using group selection. That area contained openings of 0.40–4.05 ha where all but 2.3 m²/ha of overstory basal area (primarily pine) was removed, and the forest matrix surrounding those openings was thinned. Both of the preceding 2 treatments contained unharvested buffer strips (greenbelts) along ephemeral stream drains for watershed protection. Greenbelts were typically mixed pine–hardwood remnants (15–50 m wide) of mature (≥50-year-old) forest where no cutting or midstory removal was conducted. A 1,791-ha unit was managed using a mix of treatments and silvicultural systems, including single-tree selection, group selection, and seed-tree cuts. The basin also contained an 836-ha, largely untreated, experimental forest consisting mostly of mature, 2nd-growth pine–hardwood stands. Throughout the basin, unharvested stands were interspersed within these treatment units. Thus, with its diversity of management approaches and intensities stemming from mixed ownership, the Winona Basin contained most of the predominant forest types, stand conditions, and forest management practices that existed in the Ouachita Mountains.

Capture and telemetry of bats.—During 107 nights, from 15 May until 27 July (hereafter, summer) 2000–2005, we captured bats between 2100 and 0130 h Central Standard Time using 3–8 mist nets (2.6–12.0 m wide × 2.6 m tall) at 11 trapping areas distributed throughout the basin. We assessed age of bats (juvenile or adult) based on degree of ossification of metacarpal–phalanx joints (Racey 1974), and reproductive condition of females was determined by abdominal palpation and inspection of mammae (Kunz 1988).

We used 0.25- or 0.32-g radiotransmitters (Blackburn Transmitters, Nacogdoches, Texas) with 10- to 11-day life spans to locate bats at their diurnal roost sites from mid-May until early August. Transmitters were bonded to the mid-scapular region with surgical adhesive after partial removal of hair. Radiotransmitter load was 3.0–8.0% of body weight and averaged 5.8% ± 0.2% *SE*. Although mean radiotransmitter loads slightly exceeded the recommended 5% (Aldridge and Brigham 1988), mass of transmitters was substantially lower than the 0.45-g transmitters used in previous studies of pipistrelles (Carter et al. 1999; Veilleux et al. 2003). Furthermore, Kurta and Murray (2002) found that radiotransmitters weighing 8% of body mass did not adversely affect Indiana myotis (*Myotis sodalis*). All instrumented bats were adults except for 1 female and 1 male. We instrumented those 2 juveniles to locate maternity colonies, which were scarce in our study. We treated the juvenile male as female in analyses because it roosted with another bat that we believed was its mother. 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 radiotracked each bat to its roost site the morning after capture and approximately 5 days/week. Once the approximate roost tree was determined, we located bats either from the ground using binoculars or by climbing the tree while being careful not to disturb roosting bats. However, when a roosting bat could not be visually located in the tree, we collected habitat data for the general area (hereafter, roost site) indicated by radiotelemetry, but we did not collect data specific to the roost tree (e.g., tree species).

Collection of roost and site data.—For visually confirmed roosts, we recorded tree species, dbh (cm), and distance (m) to nearest overstory tree from roost tree. We measured roost height (m), total tree height (m), and height to base of tree canopy (m) with a clinometer. An index of canopy volume was estimated by measuring canopy width in 2 dimensions (90° apart) on the ground; widths were then multiplied by canopy height (total height − height to base of canopy). Percent canopy closure from roost to 2 m above and from roost to 2 m below was independently estimated by 2 observers and averaged.

To characterize habitat surrounding each roost, we collected site attributes within a 17.84-m-radius (0.1-ha) plot centered on the roost tree (e.g., Brigham et al. 1997). For roosts that lacked visual confirmation (6.1% of roosts) this plot was centered on the general area indicated by radiotelemetry. At each plot, we determined pine and hardwood overstory heights (m) by averaging heights for 2 dominant pines and 2 dominant hardwoods. Within the plot, all woody stems > 1 m tall and < 5 cm dbh were counted, all woody stems > 1 m tall and ≥ 5 cm dbh were recorded by dbh and species, and all stumps with ≥10-cm-diameter tops resulting from recent harvesting were tallied. At 4 locations (90° apart) along the outer edge of the plot, we measured canopy cover using a spherical densiometer and pine and hardwood basal area using a 1-factor metric prism; data for each variable were then averaged for the plot.

To determine potential site characteristics that may have affected roost selection, we selected random trees and associated

site plots for comparison with roost trees and site plots. Identical habitat measurements were collected for random and roost plots. To ensure random trees were among those available to bats, we selected a random tree for each roost tree by choosing the 1st tree $\geq$ 5 cm dbh (hardwood or pine) and > 40 m distance, at a random azimuth from the roost location. When adjacent roost locations were $\leq$20 m apart ($n = 5$ roosts), we measured a single plot (centered between the 2 roosts) and a single corresponding random plot.

Data analysis.—We used roosts as the experimental unit; we assumed that individual preferences for day roosts did not bias our results and that roost trees were independent observations. We compared proportions of tree species used for roosting with proportions of available trees $\geq$ 5 cm dbh from random plots using chi-square goodness-of-fit tests for males and females separately. For those tests, we classified roost and random trees into 6 groups: oaks, hickories, pines, dogwoods (*Cornus florida*), maples (*Acer rubrum*), and other hardwood species. All statistical tests were conducted at $\alpha = 0.05$.

To determine if pipistrelles selected roost trees based on specific tree characteristics (e.g., height or diameter), we compared characteristics of trees selected by males and females with random trees using univariate analysis of variance (ANOVA; PROC MIXED—Littell et al. 1996). We did not include 1 roost in a tree < 5 cm dbh (sapling) because only trees $\geq$ 5 cm dbh were included in our random tree samples. In addition, 4 roosts (1 female and 3 male) in recently dead trees (snags that still held dead leaves) were not included in comparisons of roost tree characteristics because we did not include snags as random trees. However, those roosts were included in the analyses of roost attributes (e.g., roost height), tree species, and sites.

To determine how forest attributes affected roost selection, we used matched-pairs (each roost matched with its random location) conditional logistic regression (Hosmer and Lemeshow 2000) to create models that related habitat parameters with an increased likelihood of bat roosting. We analyzed attributes surrounding roosts only for males because samples sizes for females limited our ability to create accurate models. We included 10 habitat parameters (Table 1) derived from 0.1-ha plots surrounding roost and random trees in analyses after removing variables that were highly correlated ($r \geq 0.70$). We then determined a set of candidate models 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 Inc. 2000). Finally, we determined the most-parsimonious model among all candidate models based on the value of Akaike's information criterion (Burnham and Anderson 2002) modified for small samples (AIC$_c$—Anderson et al. 2000). We used multimodel inference by averaging parameter estimates and standard errors of models within 2 units of AIC$_{min}$ (Burnham and Anderson 2002); we used weights (ω_i) calculated among models within 2 units of AIC$_{min}$ for averaging and we calculated odds ratios from averaged parameters. Odds ratios were odds of roost/odds of random. We computed unconditional standard errors for each parameter (Burnham

TABLE 1.—Site characteristics from 0.1-ha plots entered into logistic regression models comparing roost sites of male eastern pipistrelles (*Perimyotis subflavus*) with random locations in the Ouachita Mountains of Arkansas, 2000–2005. dbh = diameter at breast height.

Variable	Description
PTH	Average tree height of pines (m)
HTH	Average tree height of hardwoods (m)
BAp	Average overstory basal area of pines (m^2/ha)
BAh	Average overstory basal area of hardwoods (m^2/ha)
COV	Average overstory canopy cover (%)
DisTree	Distance to nearest tree (m)
Under5	No. of stems < 5 cm dbh (total number in plot)
H5to25	No. of hardwoods 5–24.9 cm dbh (total number in plot)
H>25	No. of hardwoods $\geq$ 25 cm dbh (total number in plot)
P5to25	No. of pines 5–24.9 cm dbh (total number in plot)

and Anderson 2002), and evaluated overall model fit using a generalized maximum-rescaled R^2 (Nagelkerke 1991).

We compared proportions of used habitats with proportions of available habitats using chi-square goodness-of-fit tests. We defined available habitat based on locations of roosts by creating a 1,000-m buffer around each roost location. We then created a polygon that encompassed all buffers; that polygon was the area of available habitat. Although little information is available on home ranges or movements by pipistrelles, the 1,000-m buffer corresponded roughly with the average distance between roost locations and foraging areas for a pipistrelle in Georgia (1,137 m—Krishon et al. 1997). We created separate habitat availability polygons for males and females and compared use and availability separately. Forest habitat classes were derived from forest stand maps of the study area obtained from the Ouachita National Forest. Those maps were updated and corrected using a 10-m digital color orthoquad and ground-truthing. We collected global positioning system coordinates for each roost location and overlaid those locations on vegetation maps to determine the proportion of roosts in each habitat type.

RESULTS

Over the 6 summers, we captured 59 pipistrelles (7.8% of all bat captures) during 494 net-nights. Eighty-three percent of pipistrelle captures were males and 17% were females. We instrumented 28 males and 9 females, but 7 of those males and 2 females were never detected after release. For the remaining 28 bats (21 male and 7 female), we located 49 roosts (33 male and 16 female). Of those, 46 roosts (32 male and 14 female) were visually confirmed. Number of roosts per bat was 1–3 (1.65 $\pm$ 0.17 *SE*) for males and 1–5 (2.0 $\pm$ 0.53) for females. At the time of instrumentation, 2 of the 7 female bats were pregnant, 4 were lactating, and 1 juvenile was not reproductive.

For combined sexes, most (78%) roosts were in dead leaves of deciduous trees (Table 2). Seven roosts of females (50%) were in dead leaf clusters of live or recently dead trees that still held dead leaves. Three maternity colonies were in canopies of

TABLE 2.—Number of roosts of eastern pipistrelle males and females (delineated by solitary or colonial roosts) in live or dead vegetation, by tree species, and composition of tree species ≥ 5.0 cm diameter at breast height (dbh) in random plots of the Ouachita Mountains of Arkansas, 2000–2005.

| | Males[a] | | Females | | | | Tree composition in random plots (%)[b] |
| | | | Live | | Dead | | |
Species	Live	Dead	Solitary	Colony	Solitary	Colony	
Quercus alba		13		2	3		23.8
Q. rubra		9			1		2.0
Q. stellata		1		1	1		2.2
Q. velutina		4			1	1	3.8
Carya texana		1					3.4
Liquidambar styraciflua	1	1	1				3.2
Ostrya virginiana	1						2.3
Pinus echinata						3	19.4

[a] One additional roost of a male was in the live vegetation of a sapling *Ilex opaca* < 5.0 cm dbh.

[b] Composition of available tree groups was 34% oaks, 9% maples, 19% pines, 10% hickories, 4% dogwoods, and 24% other hardwoods.

live overstory pines; 1 was located on a limb surrounded by dead pine needles and 2 were located in clusters of dead pine needles that had accumulated on limb crotches. All other roosts were in hardwoods. Most dead leaf clusters in deciduous trees were brown; however, 1 female roosted in a recently dead leaf cluster that was still green but darker than surrounding leaves. One maternity colony consisted of each individual (with pups) located in a different leaf cluster on the same dead limb. Nine of 14 female roosts were confirmed maternal roosts, and 7 of these were colonies (roosts containing ≥2 adult bats; Table 2). Seven female roosts were solitary, and 2 of those held a single female and pup. Based on exit counts and counts of visible pups in roosts, estimated number of bats (adults and pups) in colonies was 3–13 and averaged 6.9 ± 1.5.

All adult males roosted alone, and 91% of roosts were in dead leaves of deciduous trees (Table 2). Dead leaves used for roosting ranged from 1 leaf to clusters of leaves approximately 20 × 30 cm. Leaf clusters were typically on small (< 1.5-cm-diameter) broken branches that hung below or on the edge of tree canopies. Although male pipistrelles changed roosts during

the period of radiotracking, some individuals showed a high degree of site fidelity to a particular leaf cluster. For example, 1 male roosted in the same cluster of leaves for 33 days, and another individual roosted in a cluster for 23 days.

For both sexes combined, 80% of roosts were in oaks. Composition of available trees ≥ 5.0 cm dbh in random plots was 34% oaks, 9% maples, 19% pines, 10% hickories, 4% dogwoods, and 24% other hardwood species. The proportion of trees used by males for roosting was 87% oaks, 3% hickories, and 10% other hardwood species, which differed from proportions of random trees ($\chi^2 = 39.7$, $d.f. = 5$, $P < 0.001$). The proportion of trees used by females for roosting was 71% oaks, 21% pines, and 7% other hardwood species, which did not differ significantly from proportions of available random trees ($\chi^2 = 10.6$, $d.f. = 5$, $P = 0.060$).

Size of trees used for roosting by males did not differ from random; however, females roosted in trees that were taller, greater in diameter, and higher to the base of crown than both roost trees of males and random trees (Table 3). Males roosted at lower heights than females. Canopy closure above and below

TABLE 3.—Attributes of roosts of eastern pipistrelles in live trees[a] and ANOVA comparisons among attributes of roosts of males, roosts of females, and random trees in the Ouachita Mountains of Arkansas during summer, 2000–2005. dbh = diameter at breast height.

| | Female | | Male | | Random | | | |
Attributes	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	F	P
Tree characteristics[b]								
Tree height (m)	21.7a[c]	0.5	15.1b	0.9	14.1b	1.0	9.94	<0.001
Tree dbh (cm)	30.7a	1.6	19.7b	1.6	19.8b	1.8	6.78	0.002
Height to base of canopy (m)	11.0a	0.9	6.3b	0.6	6.7b	0.7	8.09	<0.001
Canopy volume (m³)	651	142	365	55	361	89	1.93	0.152
Roost characteristics[d]								
Height to roost (m)	16.7	0.6	9.9	0.8			28.9	<0.001
Canopy closure above roost (%)	70.3	8.3	55.3	6.0			2.04	0.161
Canopy closure below roost (%)	13.6	6.9	29.6	7.2			1.89	0.177

[a] Does not include 4 roosts (1 female and 3 male) in recently dead snags.

[b] Includes only roosts in trees ≥ 5 cm dbh ($n = 28$ roosts for 20 males and 13 roosts for 7 females).

[c] Within rows, means with like letters were not significantly different using Tukey–Kramer adjustments to separate means ($\alpha = 0.05$).

[d] Includes 1 additional roost in a tree < 5 cm dbh.

TABLE 4.—Values of Akaike information criterion modified for small samples (AIC_c), difference from AIC_{min} (Δ_i), model weights (ω_i), and generalized R^2 for models within 2 units AIC_{min} (32.243) that explained differences between roost sites of male eastern pipistrelles and random locations in the Ouachita Mountains of Arkansas, 2000–2005. Model parameters are defined in Table 1[a].

Model	AIC_c	Δ_i	ω_i	R^2
PTH + BAp + H5to25	32.406	0.163	0.357	0.47
PTH + BAp + H5to25 + DisTree	33.067	0.824	0.256	0.52
PTH + BAp + H5to25 + DisTree − COV	32.243	0.000	0.387	0.61

[a] + = positive association with roost location in model; − = negative association.

TABLE 5.—Percent of roosts for male ($n = 33$ roosts) and female ($n = 16$ roosts) eastern pipistrelles in 6 forest habitats and percent of each habitat available in the Ouachita Mountains of Arkansas, 2000–2005.

Habitat	Male		Female	
	Used	Available	Used	Available
Mixed pine−hardwood group selection	21.2	14.2	0.0	25.5
Mixed pine−hardwood, partially harvested	27.3	28.7	6.3	12.8
Unharvested hardwoods 50−99 years old	18.2	10.3	68.7	8.7
Unharvested mixed pine−hardwood 50−99 years old	27.3	16.8	12.5	10.1
Unharvested mixed pine−hardwood ≥ 100 years old	6.1	6.0	12.5	10.1
Other habitats	0.0	24.0	0.0	32.8

roosts did not differ between males and females (Table 3); both sexes selected roosts with dense vegetation above and more open conditions below the roost.

For males, 3 models were within 2 units of AIC_{min} (Table 4). The parameter-averaged model included the following variables: PTH (estimate = 0.694 ± 0.323 *SE*; odds ratio = 0.948), BAp (estimate = 0.502 ± 0.295; odds ratio = 1.652), COV (estimate = −0.054 ± 0.047; odds ratio = 0.948), DisTree (estimate = 0.395 ± 0.303; odds ratio = 1.485), and H5to25 (estimate = 0.083 ± 0.061; odds ratio = 1.087). Males were more likely to roost at sites with more large pines in the overstory (PTH and BAp), more midstory hardwoods (H5to25), lower canopy cover (COV), and in trees farther from the nearest overstory tree (DisTree) than random locations.

Roosts were located only in forest stands that were dominated by mature (≥ 50-year-old) overstory trees and contained a hardwood component (Table 5). Proportions of habitats used for roosting by males differed from available proportions ($\chi^2 = 12.29$, *d.f.* = 5, $P = 0.031$), with most (52%) roosts of males in unharvested, mature stands ≥ 50 years old. Although 27% of roosts of males were in partially harvested, mixed pine–hardwood stands, 89% of those roosts were located in or on edges of unharvested greenbelts. Recently harvested group-selection stands also were used by males (21% of roosts), but 86% of those roosts were in greenbelts. Proportions of habitats used for roosting by females also differed from available proportions ($\chi^2 = 79.9$, *d.f.* = 5, $P < 0.001$). Most (94%) roosts of females were in unharvested pine or pine–hardwood stands ≥ 50 years old. Only 1 roost of a female was in a partially harvested stand but that roost was in a greenbelt. No roosts of females were in group-selection stands.

DISCUSSION

Both male and female pipistrelles selected roosts in live and dead vegetation in canopies of live and recently dead trees that retained dead leaves. Others have suggested that this species may roost in tree hollows in forested environments (Menzel et al. 1996; Whitaker 1998), but we found no roosts in hollow trees, cavities, or under tree bark. Pipistrelles have been observed roosting in leaves in Mexico (Findley 1954), South Carolina (Leput 2004), and Indiana (Veilleux et al. 2003). Thus, use of vegetation for diurnal roosting during summer appears to be common characteristic of this species in forests throughout its range. Although eastern red bats (*Lasiurus borealis*) are known to roost in dead leaves during winter (L. W. Robbins, pers. comm.), roosting primarily in dead leaf clusters during summer by eastern pipistrelles is likely unique among temperate North American bats. However, it is not known if this behavior occurs during other times of the year.

Veilleux et al. (2003) suggested that female pipistrelles had greater site fidelity than many other temperate foliage-roosting species, but maximum length of time in a roost was 17 days. We found that males remained in dead leaf clusters up to 33 days. Greater security from predators provided by dead leaf clusters or the more limited availability of dead leaf clusters compared with live vegetation used by other vegetation-roosting species may account for this greater site fidelity. Roosting in dead leaf clusters has obvious implications for avoiding visual predators. Clusters were usually dense enough to prevent viewing the bat from the ground, and the yellow-brown coloration of pipistrelles and similar leaf color made pipistrelles difficult to distinguish from dead leaves.

Oaks appear to be an important substrate for this species. Veilleux et al. (2003) found maples were the trees used most (32% of roosts of females), but those trees comprised 37% of available; however, 27% of roosts were in oaks, which comprised only 3% of available trees. Leput (2004) found that 86% of roosts of females in oaks. Maples comprised 9% of available trees in our study but no roosts were located in trees of that genus. For both sexes, most (80%) roosts were located in oaks, which comprised only 34% of available trees. Furthermore, 29% of roosts of males were in northern red oaks (*Quercus rubra*), which comprised only 2% of available trees. Veilleux et al. (2003) suggested that dead leaves of oaks may persist longer than those of other tree species. Oaks appear to be an important habitat component for pipistrelles in forests throughout the eastern United States. Although pipistrelles roosted primarily in deciduous hardwoods, we found that maternity colonies of females occasionally roosted in accumulated dead needles in pines. This is the 1st documented use of conifers for roosting by this species. Although Hein et al. (2005) found winter roosts of Seminole bats (*Lasiurus seminolus*) in pine needles that had accumulated in understory hardwoods, we found that female pipistrelles roosted in dead pine needles located in the canopies of large pines.

Male pipistrelles selected tree sizes randomly, whereas females selected trees that were larger than random. Preference for larger trees in the landscape has been demonstrated for other vegetation-roosting species such as eastern red bats (*L. borealis*—Hutchinson and Lacki 2000; Mager and Nelson 2001; Menzel et al. 1998) and most bats in general (Kalcounis-Rüppell et al. 2005). Roosts of female pipistrelles were at similar heights to those found by Veilleux et al. (2003) and in overstory trees of similar size to those found by others (Leput 2004; Veilleux et al. 2003). However, males in our study roosted in smaller trees than females and males frequently (16% of roosts) roosted near the ground (<5 m) but females did not. Females may be selecting day roosts higher in canopies to reduce the ability of terrestrial predators to locate their roosts visually, avoid disturbances from activities on the ground, permit young bats a greater opportunity to conduct successful initial flights, and provide thermal benefits for developing young (Constantine 1966; Vonhof and Barclay 1996). Further, dead leaves near the ground are highly susceptible to fires. Historically, natural- and anthropogenic-caused fires were a common occurrence in the Ouachita Mountains and throughout the southeastern United States (Lorimer 2001; Masters et al. 1995; Sharitz et al. 1992). Females with nonvolant pups may roost higher in trees to avoid the common subcanopy fires that historically shaped these ecosystems. Controlled burns conducted during late spring and early summer months could be detrimental to low-roosting male pipistrelles given the flammability of their roosting substrate. However, little information is available on effects of burning on the behavior of forest bats other than a few observations of bats exiting roosts in leaf litter during controlled winter burns (Moorman et al. 1999; Saugey et al. 1989).

Both sexes primarily roosted at sites that contained a mature overstory with a hardwood component, and had a complex vertical structure with abundant midstory trees. Eastern pipistrelles are considered a clutter-adapted species, and their activity is typically greater in habitats with relatively dense vertical structure (Menzel et al. 2005). Thus, it is not unreasonable to suggest that they may prefer roosting in relatively cluttered habitats also. Sites where male pipistrelles roosted were more likely to have higher densities of midstory hardwoods (5.0–24.9 cm dbh), to have more large overstory pines, to be farther from the nearest overstory tree, and to have less canopy cover than random locations. Less canopy cover at roost sites than at random locations is frequently found in studies of bat roosting (Kalcounis-Rüppell et al. 2005), and studies frequently find roost trees farther from other trees than random trees (e.g., Betts 1998; Brigham et al. 1997). We found many (33%) roosts of males in midstory or understory hardwoods of unharvested stands that were dominated by overstory pines. Thus, areas with abundant midstory oaks, especially northern red oaks, appeared to be a preferred roosting habitat for male pipistrelles.

Roosts for both sexes were located only in forest stands where the overstory was ≥50 years old and a hardwood component was present, although females occasionally roosted in pines. For females, 94% of roosts were in stands that had not recently been partially harvested and 52% of roosts of males were in those stands. Within harvested stands, all but 2 roosts were in unharvested greenbelts. Greenbelts contained abundant midstory hardwoods and vertical structure in those areas was more complex than surrounding harvested areas. Our results suggest that mature (≥ 50-year-old) forests that contain hardwoods are important to both sexes of pipistrelle bat, and unharvested inclusions that contain hardwoods in harvested areas are an important habitat component. No roost of either sex was located in industrial pine plantations, even though these stands comprised approximately 12% of the study area. However, pipistrelles were found to roost extensively in unharvested, hardwood-dominated riparian areas imbedded in pine plantations in Mississippi (D. A. Miller, pers. comm.).

Habitat selection is a hierarchical process. In the absence of preferred habitats, animals may select habitats that are suboptimal. Therefore, landscapes that lack diversity can limit or bias results of resource-selection studies and results from those studies should be interpreted carefully. Because our landscape had a diversity of forest types, stand ages, and management practices, we believe that roost associations in this study reflected actual preferences.

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