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Sex-specific roost selection by adult red bats in a diverse forested landscape

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Abstract

The eastern red bat (*Lasiurus borealis*) is a common, widespread species that occurs throughout eastern North America; however, information on potential differences in roost selection between sexes is limited. We studied summer diurnal roosting of adult red bats in a diverse forested landscape to: (1) characterize roosts of adult males and females, (2) determine habitat relationships for both sexes, and (3) compare roost selection between the sexes. We radiotracked 21 male and 20 female red bats to 142 roost locations and quantified roost characteristics. Both sexes roosted mostly in overstory hardwoods (82% of male and 81% of female roosts), but males occasionally (8% of roosts) roosted in sapling (<5 cm diameter at breast height; dbh) whereas females did not. Females roosted at greater heights than males but, mean diameter and height of roost trees $\geq$5 cm dbh did not differ between sexes; roosts trees used by both sexes were greater in diameter and height than random trees. We found no difference between sexes in tree species used for roosting; both sexes preferred to roost in white oaks (*Quercus alba*) and hickories (*Carya* spp.) but avoided Pines (*Pinus* spp.). Sex-specific habitat models created using an information-theoretic approach indicated males were more likely to roosts at sites with more midstory (5–10 cm dbh) and small overstory (10–25 cm dbh) hardwoods, taller hardwoods, shorter pines, and further from the nearest tree than random. Females were more likely to roost at sites with more midstory hardwoods, fewer small overstory pines (10–25 cm dbh), and fewer understory (<5 cm dbh) woody stems than random. Comparisons of mean habitat parameters surrounding roost sites indicated only distance to nearest tree differed ($P < 0.05$) between sexes; females roosted further from the nearest tree than males. Ninety-five percent of male roosts and 92% of female roosts were in stands dominated by mature ($\geq$50 years old) trees, and 45% of male roosts and 40% of female roosts were in stands that had been partially harvested 1–5 years earlier but retained mature overstory hardwoods. Retaining minimum basal areas of 1.1–2.3 m^2/ha of overstory hardwoods and retaining unharvested buffers along stream drains in harvested areas would likely provide adequate roosting habitat for both sexes of red bats in managed landscapes during summer.
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1. Introduction

Forest management alters the structure and function of forests and these alterations can often affect species that rely on forests for the resources needed to sustain viable populations. In forested ecosystems, bats rely on a variety of structural and spatial components such as snags or large overstory trees for roosting and canopy gaps for foraging. In the life history of bats, roosts and food are the two most important resources known to affect bat distribution and abundance (Kunz and Lumsden, 2003). Roosts provide protection from predators, thermoregulatory benefits, and places to raise young and interact socially (Kunz and Lumsden, 2003).

The eastern red bat (*Lasiurus borealis*) is an insectivorous bat that is widely distributed throughout a large portion of North America (Shump and Shump, 1982). It is the most frequently captured forest-dwelling bat in most of Arkansas (Baker and Ward, 1967; Gardner and McDaniel, 1978; Saugey et al., 1989). Because of their abundance and insectivorous diet, red bats likely play important roles in forested ecosystems by consuming forest pests and reducing disease-carrying insects. However, red bat ecology has received little attention until recently.

Bat of the genus *Lasiurus* roost primarily in tree foliage, and during summer, red bats typically roost among deciduous leaves in tree canopies (e.g., Hutchinson and Lacki, 2000; Menzel et al., 1998). Other than females with young, both sexes

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usually roost alone (e.g., Hutchinson and Lacki, 2000). In both urban and forested environments, red bats roost mostly in overstory hardwoods (e.g., *Quercus* spp. and *Carya* spp.; Hutchinson and Lacki, 2000; Menzel et al., 2000; Mager and Nelson, 2001; Limpert et al., 2007).

Recently, studies of red bat roosting have become more plentiful. However, to discern ubiquitous traits of a species from those limited to certain geographic areas, multiple studies from a diversity of ecotypes and geographic locations are required to fully understand the range of habitat tolerances of a species. Furthermore, inferences from studies are usually limited by geographic or ecological conditions of the study area. For example, Hutchinson and Lacki (2000) quantified red bat roosting in an area of hardwood forest that was largely undisturbed by silvicultural activities, Elmore et al. (2004) quantified roosting in an area of industrial timberlands comprised mostly of intensively managed pine (*Pinus* spp.) stands, and Mager and Nelson (2001) quantified red bat roosting in an urban environment. Therefore, to develop effective conservation of bats, multiple studies from a variety of landscapes are essential.

Because males of many cavity-roosting forest bats typically roost alone whereas females roost in colonies during summer (e.g., Broders and Forbes, 2004; Miles et al., 2006), sex-specific differences in roost selection might be expected for those species. However, potential differences in roost selection between sexes of *Lasiurus* (which typically roost alone) are not obvious. During summer, females may select roosts that differ from males because of added physiological requirements associated with reproduction, lactation, and avoidance of predators when pups are nonvolant, but most previous studies of red bat roosting ecology pooled data across age and sex classes largely because of small sample sizes ($\leq$14 individuals; e.g., Hutchinson and Lacki, 2000; Menzel et al., 2000; Mager and Nelson, 2001). Thus, information on potential differences in roosting ecology between sexes of red bats is needed.

Our objectives were: (1) characterize roost selection by adult male and female red bats in a diversely forested landscape of Arkansas, (2) determine habitat relationships for both males and females, and (3) compare male and female roost selection. We compared roost trees and surrounding sites between sexes and with random trees and sites.

2. Methods

2.1. Study area

We conducted the study in the 6545-ha Upper Lake Winona Basin, situated in northwestern Saline County (34°48′N, 92°58′W) in the Ouachita Mountains of central Arkansas, USA. The Ouachita Mountains are a series of east–west oriented ridges and valleys that extend from central Arkansas into east-central Oklahoma. Elevations in the region range from 152 to 853 m, mean annual precipitation ranges from 112 to 137 cm, and mean annual temperature ranges from 13.9 to 16.1 °C (Skiles, 1981).

No residential areas, houses, or agricultural lands exist in the study portion of the Winona Basin. Most of the basin consists of mixed shortleaf pine (*P. echinata*)—hardwood forests managed by the Forest Service, U.S. Department of Agriculture (Ouachita National Forest). The basin also contains a mix of other forest types, primarily oak (*Quercus* spp.)—hickory forests. Twelve percent (778 ha) of the area is intensively managed industrial timberlands consisting primarily of closed canopy and older thinned loblolly pine (*P. taeda*) plantations. These plantations were generally thinned at about 12–15 years of age and managed on a 30–35-year saw-log rotation.

National forest lands in the basin were divided into six 513–1791-ha management units where different silvicultural treatments were implemented in 2000 (Perry et al., 2007). A 1232-ha pine-grassland restoration unit was initially thinned in 2000; goal of this restoration is to create open woodland conditions maintained by periodic prescribed burning. That area was thinned to 13.8 m^2/ha overstory basal area (BA), of which 1.1 m^2/ha was retained overstory hardwoods (mostly oaks and hickories). An 864-ha single-tree selection unit was also thinned to 13.8 m^2/ha of overstory BA with 2.3 m^2/ha of that being retained hardwoods. Both of the previous 2 treatments underwent partial midstory removal whereby most hardwoods < 15 cm dbh were felled. The study area also contained a 1044-ha group selection unit where openings of 0.40 to 4.05 ha were created in the forest canopy; pines in the forest matrix surrounding those openings were thinned to about 16.0 m^2/ha of overstory BA, but no hardwoods were removed in the matrix. A 1791-ha unit was managed using a mix of treatments and silvicultural systems, including single-tree selection, group selection, and seed-tree cuts in stands of approximately 16 ha. Single-tree selection, group selection, pine woodland restoration areas, and the mixed-management area were all prescribe burned in winter 2000–2001. Harvested stands on Forest Service lands contained unharvested 15–50-m wide buffer strips (greenbelts) around stream drains for water-quality protection. Greenbelts were typically mixed pine-hardwood or hardwood forest containing mature ($\geq$50 years old) trees and no cutting or midstory removal was conducted in greenbelts. The basin also contained an 836-ha, largely untreated area consisting mostly of mature, second-growth pine-hardwood timber. Throughout the basin, unharvested stands were interspersed among these treatment units. Thus, with its silviculture treatment units, untreated areas, and industrial plantations, the Winona Basin contained most of the predominant forest types and forest management practices that existed in the Ouachita Mountains.

2.2. Bat capture and radiotelemetry

We captured red bats between 21:00 and 01:30 h CST using 3–8 mist nets (2.6–12.0 m wide × 2.6 m tall) at 10 trapping locations distributed throughout the study area. Age (juvenile or adult) was assessed based on degree of ossification of metacarpal–phalanx joints (Racey, 1974) and female reproductive condition was determined by abdominal palpation and by mammae inspection. 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 0.32–0.71-g radiotransmitters with 11–21-day life spans to locate bats at their diurnal roost sites from mid-May to early August, 2000–2004. We attached radiotransmitters to the mid-scapular region with surgical adhesive following partial hair removal. With the possible exception of one female with equivocal joint ossification, all instrumented bats were adults. We radiotracked each bat to its roost site the morning following capture and approximately 5 days/week. Once the approximate roost tree was determined, we attempted to visually locate bats from the ground using binoculars or by climbing trees. If roost trees could not be visually confirmed, we collected habitat data for the surrounding site but not the roost tree because we found that using radiotelemetry alone to identify the correct roost tree was inaccurate, especially in areas with dense and overlapping tree canopies.

2.3. Roost and site data collection

For visually confirmed roosts, we recorded tree species, dbh (cm), and aspect of roost in relation to the tree trunk. We measured roost height (m), total tree height (m), and height to base of tree canopy (m) with a clinometer. We estimated canopy volume by measuring canopy width in 2 dimensions (90° apart) on the ground and then multiplying these widths by total canopy height (total height − height to base of canopy).

To characterize habitat surrounding each roost, we collected data (site attributes) in a 17.84-m radius (0.1 ha) plot centered on the roost tree. For roosts that were not visually confirmed, this plot was centered on the general area indicated by radiotelemetry. At each plot, we recorded heights of overstory pines and hardwoods by averaging heights for 2 dominant trees from each group. We tallied all woody stems >1 m tall and <5 cm dbh in the 0.1-ha plot, and we recorded all woody stems >1 m tall and ≥ 5 cm dbh by diameter and species. At 4 random locations (90° apart) along the plot periphery, we measured canopy coverage (%) using a spherical densiometer; data from these four points were averaged for each plot.

To identify site attributes 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 that random trees and sites were available habitat for selection, we selected random trees by choosing the first tree >5 cm dbh and >40 m distance, at a random azimuth from each roost location. Because red bats in mixed pine-hardwood areas rarely roost in pines (e.g., Menzel et al., 2000), we selected only hardwood random trees. When roost trees were ≤ 20 m apart, we measured a single plot (centered between 2 roosts) and a single corresponding random plot.

We collected global positioning system (GPS) coordinates for each roost location and overlaid those locations on vegetation maps in a geographic information system (GIS) to determine the proportion of roosts in each forest habitat class. Forest habitat classes (Perry et al., 2007) were derived from ONF forest stand maps of the study area, which were updated and corrected using a 10-m digital color orthoquad (DOQ) and ground truthing. Because single-tree selection stands and pine-woodland restoration areas were in the early stages of development and were treated initially with similar partial harvesting, midstory removal, and burning in 2000, those two treatments were grouped into a single "partially harvested/thinned" class. We defined available habitats based on locations of roosts by creating a 1000-m radius circle around each roost location. We then combined all circles and designated the area within this polygon the available habitat. The 1000-m radius circle (314 ha) corresponded roughly with the average maximum distance traveled by red bats during foraging in forested environments of the southeastern U.S. (Elmore et al., 2005).

2.4. Analysis

We treated each roost location as an independent sample although multiple roost locations from individual bats were included in the data set, which is the method of analysis used in previous studies of roost selection by red bats (e.g., Menzel et al., 1998; Hutchinson and Lacki, 2000; Mager and Nelson, 2001; Elmore et al., 2004; Limpert et al., 2007). We compared characteristics of male roost trees, female roost trees, and random trees using analysis of variance (ANOVA; PROC MIXED; Littell et al., 1996). We excluded roosts in trees/shrubs <5 cm dbh ($n = 5$) because we selected only trees ≥ 5 cm dbh for random trees. We compared height of roost between males and females using a t-test. We compared roost aspect with random orientation for males and females separately using Rayleigh's test (Zar, 1999). All tests were conducted at alpha = 0.05.

We compared proportions of roosts in each tree species between males and females using Fisher's exact test and found no difference ($P = 0.456$). Therefore, we combined sexes to compare use with availability of tree species. We compared the proportion of roosts in each tree species with randomly available proportions using binomial tests. We included only roost and random trees ≥ 10 cm to make our results comparable with other studies of red bat roosting (e.g., Elmore et al., 2004; Mager and Nelson, 2001), and we included only trees from random plots associated with roost trees used in the analysis ($n = 100$ roost trees and trees from 100 random plots).

We used matched-pairs (each roost matched with its random location) conditional logistic regression (Hosmer and Lemeshow, 2000) to relate vegetation surrounding roosts with an increased likelihood of bat roosting. We created models for males and females separately. Variables that correlated ($r \geq 0.70$) with other variables were removed or combined with other variables; thus, we included 11 vegetative parameters (Table 1) derived from 0.1-ha plots surrounding roost and random trees. Variables were combined to create candidate models using a best subsets procedure, which selected the best 1-variable model, 2-variable model, and so forth based on values of the chi-square statistic (SAS Institute Inc., 2000). We determined the most parsimonious model among all candidate models based on the value of Akaike's

Table 1
Site attributes from 0.1-ha plots entered into logistic regression models comparing roost sites of male and female red bats with random locations in the Ouachita Mountains of Arkansas, 2000–2004

Attribute	Description
PTH	Average pine tree height (m)
HTH	Average hardwood tree height (m)
COV	Average overstory canopy cover (%)
DisTree	Distance to nearest tree (m)
Under5	Number of woody stems <5.0 cm dbh (total number in plot)
H5to10	Number of hardwoods 5.0–9.9 cm dbh (total number in plot)
H10to25	Number of hardwoods 10.0–24.9 cm dbh (total number in plot)
H≥25	Number of hardwoods ≥25.0 cm dbh (total number in plot)
P5to10	Number of pines 5.0–9.9 cm dbh (total number in plot)
P10to25	Number of pines 10.0–24.9 cm dbh (total number in plot)
P≥25	Number of pines ≥25.0 cm dbh (total number in plot)

Information Criterion modified for small samples (AIC_c; Burnham and Anderson, 2002). We used multimodel inference by averaging parameter estimates of models within 2 units of $\text{AIC}_{\min}$ (Burnham and Anderson, 2002); we used weights (ω_i) calculated among all models within 2 units of $\text{AIC}_{\min}$ for averaging and calculated odds ratios from averaged parameter estimates. Odds ratios were the odds of roost/random. We computed weighted unconditional standard errors for each parameter in parameter-averaged models (Burnham and Anderson, 2002), and we evaluated model strength using a generalized maximum-rescaled R^2 (Nagelkerke, 1991).

3. Results

We captured 279 red bats, which comprised 58% of all captures; 55% were males and 45% were females. We located 142 roosts (69 male and 73 female) from 42 bats (21 males and 20 females). Of these, we visually confirmed bats in 119 roosts (61 male and 58 female roosts), and 109 (60 male and 49 female) of those had corresponding random trees. Number of roosts per individual ranged from 1 to 7 (mean = 3.2, S.E. = 0.39) for males and from 1 to 7 (mean = 3.0, S.E. = 0.41) for females. At the time of capture, 6 of 20 females were pregnant, 10 were lactating, 3 were post-lactating, and reproductive status of 1 was unknown. We confirmed that 62% ($n = 36$) of female roosts were maternal (pups present); however, pups could not be seen with 4 of the lactating females. For the 13 females that had pups visible in roosts, average number of pups was 1.77 ± 0.20 S.E. (range 1–3). Males roosted alone, although we discovered one male aggregation; in late May, we tracked an adult male to a small hickory (19.7 cm dbh) where at least three other male (based on pelage color) red bats were roosting. Each of these males roosted on a separate branch, >1 m apart.

Most male (82%) and female roosts (81%) were in overstory hardwoods; 18% of male roosts and 16% of female roosts were in midstory or understory hardwoods. Both male and female roost trees were significantly taller, greater in diameter, and had higher crown bases than random trees (Table 2). Although female roost trees were generally taller and greater in diameter than males roost trees, these differences were not significant ($P > 0.05$; Table 2). Five roosts used by 3 males (8% of male roosts) were in saplings (trees <5 cm dbh); no females roosted in saplings. An atypical roost by a female was in a blackberry (*Rubus* spp.) shrub away from its pups, but the bat died of unknown causes soon after it roosted at that location and was therefore not included in the analyses. When male sapling roosts were included, average tree height for males was 15.7 m (S.E. = 0.7), which was not lower than tree heights for females (Student's *t*-test; $t = 1.79$, $P = 0.076$). However, with sapling roosts included males roosted at lower heights (mean = 11.9 m ± 0.6 S.E.; $P = 0.014$) than females (mean = 14.4 m ± 0.8 S.E.). Aspect of roosts did not differ from random orientation for males ($z = 0.31$, $n = 61$, $P > 0.50$) or females ($z = 1.82$, $n = 58$, $P > 0.10$).

There was no difference between males and females for tree species used for roosting ($P = 0.456$). For combined sexes, red bats used 13 species of tree ≥10 cm dbh (Table 3). Although pines (mostly shortleaf) were the most abundant trees ≥10 cm dbh in random plots, only 2 roosts (from the same nonreproductive female) were in pines; all other roosts were in foliage of deciduous hardwoods. White oaks were the most used species (37% of roosts). Based on availability, red bats preferred white oaks and hickories and avoided pines. Trees <10 cm dbh used by males for roosting included one *Q. marilandica* (blackjack oak), three *Acer rubrum* (red maple), one *Cornus florida* (dogwood), one white oak, and one *Q. velutina* (black oak). The only female roost tree <10 cm dbh was in a hickory.

Logistic regression differentiating roost sites from random sites for females included 3 models within 2 units of $\text{AIC}_{\min}$ (Table 4). The parameter-averaged model for females included the following variables: Under5 (estimate = −0.007 ± 0.003 [unconditional S.E.]; odds ratio = 0.993), H5to10 (estimate = 0.027 ± 0.012; odds ratio = 1.027), and P10to25 (estimate

Table 2
Attributes of roost trees[a] used by male and female red bats and comparisons with random trees in the Ouachita Mountains of Arkansas during summer, 2000–2004

Tree attributes	Female		Male		Random		F	P[b]
	Mean	S.E.	Mean	S.E.	Mean	S.E.		
Tree height (m)	17.6a[c]	0.8	16.8a	0.5	14.8b	0.5	6.11	0.003
Tree diameter (dbh, cm)	27.1a	1.8	26.1a	1.3	21.7b	1.1	5.28	0.006
Height to base of canopy (m)	9.2a	0.6	8.1a	0.3	6.3b	0.3	17.36	<0.001
Canopy volume (m^3)	668	109	625	71	496	57	1.57	0.210

[a] Because of missing data and only roosts in trees ≥5 cm dbh were included, $n = 55$ male and 48 female roosts.

[b] Probability of F based on ANOVA.

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

Table 3

Species composition of trees (≥10 cm dbh) in 0.10-ha random plots ($n = 1798$ trees) compared with composition of roost trees (≥10 cm dbh) used by 17 male and 18 female red bats in the Ouachita Mountains of Arkansas during summer, 2000–2004

Tree species	Composition in random plots (% of total)[a]	Number of roosts	Z[b]	P
Pinus spp.[c]	1354 (37.6)	2	−7.34	<0.001
Quercus alba	903 (25.1)	37	2.74	0.006
Carya spp.[d]	356 (9.9)	31	7.06	<0.001
Q. rubra	224 (6.2)	8	0.75	0.455
Nyssa sylvatica	190 (5.3)	5	−0.13	0.894
Acer rubrum	137 (3.8)	2	−0.94	0.347
Q. stellata	112 (3.1)	6	1.67	0.094
Liquidambar styraciflua	85 (2.4)	3	0.39	0.695
Q. velutina	57 (1.6)	2	0.32	0.750
Other species[e]	183 (5.1)	4	−0.50	0.617
Total	3601 (100)	100		

There was no difference in composition of tree species used for roosting between males and females ($P = 0.456$).

[a] Because of missing data, $n = 100$ roost trees (≥10 cm dbh) and 100 random plots.

[b] Compared using binomial tests and a Z-approximation.

[c] Primarily *P. echinata*.

[d] Included *C. texana* and *C. tomentosa*.

[e] Additional trees (≥10 cm dbh) used for roosting included *Fraxinus pennsylvanica*, *Q. falcata*, *Ulmus alata*, and *U. rubra*.

= −0.018 ± 0.023; odds ratio = 0.982). Females were more likely to roost at sites with more midstory hardwoods (H5to10), fewer small overstory pines (P10to25), and fewer understory woody stems (Under5) than random. Based on unconditional 95% confidence intervals for parameter estimates that did not include zero, Under5 and H5to10 had significant effects on roost selection.

Logistic regression differentiating roost sites from random sites for males included 4 models within 2 units of $\mathrm{AIC}_{\min}$ (Table 3). The parameter-averaged model for males included the following variables: H10to25 (estimate = 0.054 ± 0.026 [unconditional S.E.]; odds ratio = 1.055), HTH (estimate = 0.070 ± 0.055; odds ratio = 1.073), H5to10 (estimate = 0.011 ± 0.013; odds ratio = 1.011), DisTree (estimate = 0.050 ± 0.069; odds ratio = 1.051), and PTH (estimate = −0.009 ± 0.012; odds ratio = 0.992). Males were more likely to roost at sites with more small overstory hardwoods (H10to25), more midstory hardwoods (H5to10), taller hardwoods (HTH), shorter pines (PTH), and further from the nearest tree (DisTree) than random. Based on unconditional 95% confidence intervals for parameter estimates that did not contain zero, only H10to25 had a significant effect on roost selection. Direct univariate comparisons of vegetative parameters surrounding male and female roosts indicated only distance to nearest tree (DisTree) differed significantly between male and female roost sites (Table 5); female roost trees were located further from the nearest tree than male roost trees.

Males roosted in 8 forest habitat classes and females roosted in 7 (Table 6). Ninety-five percent of male roosts and 92% of female roosts were in stands dominated by mature (>50 years old) trees, which comprised 71% of available habitat. Furthermore, 45% of male roosts and 40% of female roosts were in partially harvested or group selection stands which comprised 29% of available habitat. In partially harvested stands and group selection stands, 42% of male roosts and 59% of female roosts were located in (or on the edge of) unharvested greenbelts within those stands. Consequently, 68% of male roosts and 75% of female roosts were located in unharvested patches of forest. Five female roosts were located in hardwoods within thinned loblolly pine plantations and 3 male roosts were

Table 4

Variables included, values of $\mathrm{AIC_c}$, difference from $\mathrm{AIC}_{\min}$ (Δ_i), model weights (ω_i), and maximum-rescaled R^2 for sex-specific models within 2 units of $\mathrm{AIC}_{\min}$ comparing roost sites of red bats and random locations in the Ouachita Mountains of Arkansas, 2000–2004

Model	$\mathrm{AIC_c}$	Δ_i	ω_i	R^2
Females[a]				
−Under5	59.470	1.998	0.192	0.16
−Under5 + H5to10	57.482	0.000	0.518	0.24
−Under5 + H5to10 − P10to25	58.639	1.157	0.290	0.26
Males[a]				
+H10to25	76.180	0.983	0.237	0.13
+H10to25 + HTH	76.498	1.301	0.203	0.16
+H10to25 + HTH + H5to10 + DisTree	75.197	0.000	0.388	0.19
+H10to25 + HTH + H5to10 + DisTree − PTH	76.829	1.632	0.172	0.20

+: Positive association with roost location in model, −: negative association in model. Model parameters (site attributes) are defined in Table 1.

[a] Because of missing data, $n = 47$ female roosts and 56 male roosts.

Table 5
Comparison of site attributes (from 0.1-ha plots) surrounding diurnal summer roosts between male and female red bats in the Ouachita Mountains of Arkansas, 2000–2004

Variable	Male		Female		*t*	*P*
	Mean	S.E.	Mean	S.E.		
PTH	17.6	0.8	18.1	0.9	0.45	0.652
HTH	17.9	0.5	18.5	0.7	0.81	0.419
COV	74.8	2.5	77.9	2.4	0.90	0.372
DisTree	3.1	0.2	3.8	0.2	2.08	0.040
Under5	233.4	28.2	235.7	22.9	0.06	0.949
H5to10	28.2	3.8	29.6	3.1	0.27	0.784
H10to25	24.0	2.0	23.2	2.0	−0.29	0.775
H$\geq$25	6.4	0.6	5.9	0.7	−0.57	0.568
P5to10	2.8	0.9	2.5	0.6	−0.26	0.794
P10to25	7.1	1.2	6.9	1.1	−0.08	0.934
P$\geq$25	4.6	0.5	5.8	0.6	1.56	0.121

See Table 1 for description of site attributes.

Table 6
Number (percent in parenthesis) of roosts in 10 forest habitat classes used by male and female red bats and percent availability of each class (based on merged 1000-m radius circles surrounding each roost) in the Ouachita Mountains of Arkansas, 2000–2004

Habitat	Males	Females	Available %
P/H[a] partially harvested/thinned	24 (35)	16 (22)	16
P/H group selection	7 (10)	13 (18)	13
Unharvested P/H 50–99 years old	15 (22)	21 (29)	24
Unharvested hardwood 50–99 years old	14 (20)	8 (11)	12
Unharvested P/H > 100 years old	2 (3)		3
Unharvested hardwood > 100 years old	3 (4)	9 (12)	3
Pine 15–29 years old	3 (4)		8
Older/thinned loblolly plantation		5 (7)	7
Closed-canopy loblolly plantation	1 (1)	1 (1)	6
Other habitats			8
All habitats	69	73	

[a] P/H = mixed pine-hardwood forest.

in sapling hardwoods in a young pine-dominated stand that had not yet reached canopy closure (Pine 15–29 years old).

4. Discussion

Both sexes of red bats generally roosted in the upper canopy of deciduous hardwoods and most (approximately 80%) roosts were in overstory trees (either dominants or codominants). Heights and diameters of roost trees were generally less than those found in other studies conducted in non-industrial forested landscapes (e.g., Menzel et al., 1998; Hutchinson and Lacki, 2000; Limpert et al., 2007). Red bat preference for larger (generally overstory) deciduous trees in a landscape has been demonstrated in pine-dominated, maritime oak, hardwood, and riparian forest ecosystems of the eastern and southeastern U.S. (Hutchinson and Lacki, 2000; Menzel et al., 1998; Limpert et al., 2007) and urban settings in the Midwest (Mager and Nelson, 2001), and appears to be the norm throughout its range. We found no difference in tree size ($\geq$5 cm dbh) used for roosting between males and females, but adult males roosted at lower heights and occasionally roosted in saplings $<$5 cm dbh, whereas adult females did not. Elmore et al. (2004) found adult male red bats roosted in hardwoods of moderate diameter (average of 22 cm dbh), but adult females typically roosted in larger trees ($>$25 cm dbh). Similar to our results, Constantine (1966) found female red bats with young roosting higher in tree canopies than solitary bats, and suggested this provided greater concealment from terrestrial predators, reduced disturbances arising from activities on the ground, and provided greater leeway for juvenile bats to conduct successful initial flights. Although others have suggested that red bats roost in close proximity to dead leaf clusters in tree canopies (e.g., Hutchinson and Lacki, 2000), we did not observe this behavior.

We found no difference in preference for tree species between males and females; both sexes in the Ouachita Mountains preferred white oaks and hickories and avoided pines. In Kentucky, most red bat roosts were in hickories (Hutchinson and Lacki, 2000); in Georgia and South Carolina, they preferred white oaks (Menzel et al., 1998); in Mississippi, they used hickories and sweetgum (*Liquidambar styraciflua*) more than available (Elmore et al., 2004); in Maryland, most roosts were in sweetgum, blackgum (*Nyssa sylvatica*), and tulip poplar (*Liriodendron tulipifera*; Limpert et al., 2007); and in an urban area of Illinois, most roosts were in oaks and walnuts (*Juglans nigra*; Mager and Nelson, 2001). Thus, red bats select a variety of deciduous tree species and apparently have regional preferences for specific hardwood species.

We found 2% of red bat roosts in pines and other studies in mixed forests have found a similar small percentage; both Menzel et al. (1998) and Limpert et al. (2007) found 1.6% of roosts in pines. Although Elmore et al. (2004) found 30% of red bat roosts in pines, their study area consisted primarily of pine plantations where large overstory hardwoods were likely limited. Pines were the most abundant tree type $\geq$10 cm dbh in our study area, but were rarely used by red bats. Thus, in landscapes where both mature ($>$50 years old) pines and hardwoods are abundant, both sexes of red bats prefer hardwoods and avoid pines.

The only parameter included in parameter-averaged site-level models for both males and females was abundance of midstory hardwoods; both sexes were more likely to roosts at sites with more midstory hardwoods than random. Parameters included in models for both sexes indicated an affinity for sites with abundant hardwoods (either midstory or overstory); however, most roosts (approximately 80%) were in overstory hardwoods and 93% of roosts were in trees $>$10 cm. For males, only abundance of small (10–24.9 cm dbh) overstory hardwoods had a significant effect in the averaged model (males were more likely to selected sites with greater numbers of these trees), whereas abundance of midstory hardwoods and understory density had significant effects in the model for females; females were more likely to roost at sites with an abundant midstory and a sparser understory than random. A sparse understory has been associated with red bat roosts in other studies (Menzel et al., 2000; Limpert et al., 2007). However, understory density likely had little biological effect on roost selection; instead, the greater abundance of midstory or small overstory trees at roost sites likely caused heavy shading, which reduced plant growth in the understory around roost trees.

Comparison of site attributes between male and female roosts suggested only distance to nearest tree differed significantly between male and female roost sites. Females roosted in trees that were further from other trees than males, suggesting female roosts were more open immediately around the roost tree. Roost trees located further from other trees may receive more solar radiation (less shading). Increased temperatures at roosts may speed fetal and juvenile growth during reproduction (Racey and Swift, 1981). Among site-level models, average R^2 for males was 0.17, whereas models for females averaged 0.22, which suggests models for females had better predictive power. Similarly, logistic models used to classify red bat roost sites in Mississippi had higher correct classification rates for adult females than adult males (Elmore et al., 2004). Our data and those of Elmore et al. (2004) suggest that adult females of this species may be more selective than males in their roost selection.

Forty percent of female roosts and 42% of male roosts were in mature, unharvested, second-growth forests (either hardwood or mixed pine-hardwood), and 12% of female roosts and 7% of male roosts were in older-growth (>100 years old) stands. Roosting in unharvested, mature forests (either upland or riparian) is a common behavior of red bats (Menzel et al., 1998; Hutchinson and Lacki, 2000; Limpert et al., 2007). Therefore, studies often find greater canopy closure (e.g., Menzel et al., 2000; Limpert et al., 2007) or BA (Limpert et al., 2007) at red bat roost locations than at random sites. Average canopy closure at red bat roost sites was 92% in Georgia and South Carolina (Menzel et al., 1998), 84% in Maryland (Limpert et al., 2007), and 94% for females and 91% for males in industrial forests of Mississippi (Elmore et al., 2004). In our study, canopy closure at roost sites averaged 75% for males and 78% for females, which is lower than others have reported, likely because red bats roosted frequently in relatively open forest stands that had been partially harvested.

Although sites with abundant midstory hardwoods were used most frequently for roosting, we found 40% of female roosts and 45% of male roosts in stands that had been thinned or partially harvested 1–5 years previously; those stands included single-tree selection, group selection, and pine-woodland restoration stands. An additional 7% of female roosts were in hardwoods <20 cm dbh in thinned loblolly-pine plantations. Thus, red bats readily roosted in (or near) stands that were under active management, which included overstory reductions, midstory reductions or removal, and prescribed burning. Studies suggest many bat species prefer to roost in forest stands with lower tree density (e.g., Hutchinson and Lacki, 2000) or lower canopy coverage (e.g., Brigham et al., 1997; Kalcounis-Rüppell et al., 2005; Vonhof and Barclay, 1996). Hutchinson and Lacki (2000) found red bats (mostly females) tended to roost in stands with lower overall tree densities, but higher densities of trees >25 cm dbh; however, silviculturally thinned stands were limited in their study. On industrial timberlands, Elmore et al. (2004) found adult female red bats frequently roosted in midstory hardwoods in thinned pine plantations. Our results and those of others (e.g., Elmore et al., 2004) suggest that forested areas that have undergone thinning and mid-story removal/reduction may be readily utilized by red bats for roosting if some hardwoods ≥10 cm dbh are retained.

Although about 43% of roosts were in thinned or partially harvested stands, when roosts located in unharvested greenbelts were delineated from those in harvested portions of stands, 68% of all male and 75% of all female roosts were in (or on the edge of) patches of unharvested forest. Thus, relatively small unharvested patches with abundant overstory and midstory hardwoods, such as greenbelts located in partially harvested stands, may be used extensively by reds bats in managed pine-hardwood landscapes.

Abundant greenbelts in managed stands created heterogeneous conditions with abundant edge. Although Hutchinson and Lacki (2000) found no red bat roosts <50 m from any edge, we found red bats frequently roosted in greenbelts that were generally <30-m wide. We also found red bats preferred to roost in close proximity to partially harvested stands (Perry et al., 2007). Thus, our data do not support suggestions that red bats avoid edges. Hutchinson and Lacki (2000) found 50% of red bat roosts were within sight of canopy gaps where they frequently flew for the first 5–10 min after emergence from roosts. Therefore, red bats may roost close to (or in) open forest stands where they forage to reduce energetic demand associated with travel to more distant foraging areas. Many species of bat prefer to forage in open areas, likely because of reduced structural clutter that may impede flight (Mackey and Barclay, 1989; Burford and Lacki, 1995; Menzel et al., 2002; Owen et al., 2004).

Most previous studies of red bat roosting have combined data across sex and age status (Menzel et al., 1998; Hutchinson and Lacki, 2000; Menzel et al., 2000; Mager and Nelson, 2001; Limpert et al., 2007), but studies that combine sexes or are heavily weighted to a single sex may mask potentially important differences between sexes. We found differences in roost selection between males and females. Likewise, Elmore et al. (2004) found differences in roost sites between juvenile and adult red bats and between males and females, and other studies have found differences in roost selection between sexes of other species, such as northern long-eared bats (Broders and Forbes, 2004; Perry and Thill, 2007a). Thus, future studies should strive to separate sex and age status, or concentrate on one gender/age status and temper conclusions accordingly.

5. Management implications

Few obvious differences existed in stands selected for roosting between sexes. Comparable percentages of roosts were in harvested stands (45% male, 40% female), unharvested, second-growth stands (42% male, 40% female), and older-growth stands (7% male, 12% female). Based on the wide range of forest stand conditions that both sexes of red bats used for roosting, they are likely generalists that select stands based primarily on presence of overstory or larger (>10 cm dbh) midstory hardwoods. Although Hutchinson and Lacki (2000) suggested that large tracts of mature timber be retained in eastern North America to provide suitable habitat for red bats, our results suggest they will roost in actively managed landscapes if adequate densities (minimum BAs of 1.1 to 2.3 m^2/ha) of overstory hardwoods ($\geq$10 cm dbh) are retained in areas undergoing timber harvest in the Ouachita Mountains. Furthermore, unharvested greenbelts surrounding stream drains should be maintained for both water-quality protection and as potential habitat for red bats and other bat species such as eastern pipistrelles (*Perimyotis subflavus*; Perry and Thill, 2007b). To provide red bat habitat, Limpert et al. (2007) suggested that managers should maintain forest tracts with deciduous trees >40 cm dbh and $\geq$84% canopy cover in Maryland. However, we found mean dbh of roost trees was 26.1 cm for males and 27.1 cm for females, and mean canopy cover at roost sites was 75% for males and 78% for females (range 14–98%). Furthermore, Elmore et al. (2003) found mean hardwood diameter used for roosting by red bats was 18.1 cm and overall mean diameter (including pines) ranged from 22.8 to 27.2 depending on sex and age in Mississippi.

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