Roost selection by male and female northern long-eared bats in a pine-dominated landscape

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Abstract

We radiotracked 17 male northern long-eared bats (*Myotis septentrionalis*) to 43-day roosts and 23 females to 49-day roosts in the Ouachita Mountains of central Arkansas during summers 2000–2005. We compared characteristics of roost trees between males and females, and compared characteristics of sites surrounding roosts with random locations for each sex. Roosts were located in cavities, crevices, and under loose bark, primarily in snags; 85% of male and 95% of female roosts were in snags. Shortleaf pine (*Pinus echinata*) was the most utilized tree species (71% of roosts) and both sexes preferred ($P < 0.05$) pine snags over hardwood snags. Most (80%) snag roosts were in snags 10–24.9 cm dbh, but females roosted in snags of greater diameter than males and males tended to roost more in small (<10 cm dbh) hardwoods than females. Female roost sites were more likely to have fewer large ($\geq$25 cm dbh) hardwoods, fewer midstory pines 5–9.9 cm dbh, fewer small (<10 cm dbh) hardwood snags, more overstory pines $\geq$25 cm dbh, and more pine snags <10 cm dbh than random sites. Most (55%) female roosts were located in pine-dominated stands that had undergone partial harvesting and midstory removal. Males were more likely to select sites with abundant large ($\geq$25 cm dbh) overstory pines, fewer small overstory pines (10–24.9 cm dbh), and more large pine snags $\geq$10 cm dbh than random. More male roosts (42%) were in unharvested stands than female roosts (24%), and females roosted at sites with fewer midstory trees than males. Our results demonstrate the importance of pine snags as roosting habitat for northern long-eared bats and the importance to females of snags located in relatively open forests in the Ouachita Mountains during summer.
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1. Introduction

The northern long-eared bat is a relatively common species found throughout the northeast and north-central U.S., and southern Canada (Caceres and Barclay, 2000). The Ouachita Mountains of western Arkansas and eastern Oklahoma represent the southern periphery of this species' distribution and is one of the few pine-dominated areas of the southeastern U.S. where this species occurs (Sealander and Heidt, 1990; Caceres and Barclay, 2000). Nevertheless, northern long-eared bats are relatively plentiful in the Ouachita Mountains (R. Perry, unpublished data).

Northern long-eared bats roost in cavities, crevices, and under exfoliating bark in deciduous hardwood trees; they are occasionally found roosting in conifers (Sasse and Pekins,

1996; Foster and Kurta, 1999; Lacki and Schwierjohann, 2001; Owen et al., 2002; Menzel et al., 2002; Jackson, 2004; Jung et al., 2004; Carter and Feldhamer, 2005; Ford et al., 2006). However, most previous studies of roosting by northern long-eared bats were conducted in areas dominated by hardwood forests, and no comprehensive roosting studies have been conducted for this species in pine-dominated landscapes of the southeastern U.S.

Only recently has research begun to explore differences in roosting behavior between sexes and most previous studies of roost selection by northern long-eared bats either combined sexes (e.g., Lacki and Schwierjohann, 2001) or conducted the study on a single sex (e.g., Sasse and Pekins, 1996; Foster and Kurta, 1999; Menzel et al., 2002; Owen et al., 2002; Jackson, 2004; Carter and Feldhamer, 2005; Ford et al., 2006). Although Broders and Forbes (2004) differentiated roost selection between sexes, their study was conducted in New Brunswick and its applicability to ecosystems of the southeastern U.S. may be limited.

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Here, we characterize roosts selected by both male and female northern long-eared bats in the Ouachita Mountains of Arkansas. We compared roosts between sexes, and created separate models for males and females that distinguished vegetation characteristics of roost sites from random locations.

2. Methods

2.1. Study area

Our study was conducted 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. The Ouachita Mountains are a series of east–west oriented ridges and valleys that extend from central Arkansas into east-central Oklahoma. Elevations in this 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).

Most of the basin consisted of mixed shortleaf pine (*Pinus echinata*)-hardwood forests managed by the Forest Service, U.S. Department of Agriculture (Ouachita National Forest; ONF). The basin also contained a mix of other forest types including oak (*Quercus* spp.) – hickory (*Carya* spp.) and riparian hardwood forests. Approximately 12% (778 ha) of the study area was intensively managed industrial timberlands consisting primarily of closed canopy or older thinned plantations of loblolly pine (*Pinus taeda*), which were generally thinned and pruned at about 12–15 years of age.

National Forest lands within the basin were divided into four areas where different silvicultural treatments were implemented in 2000 (Perry et al., 2007). These included: (1) partial harvesting and midstory removal (2096 ha) with overstory basal areas (BA) of 13.8 m^2/ha pine and 1.1–2.3 m^2/ha hardwood; (2) group selection (1044 ha) where groups or trees were removed in openings of 0.40–4.05 ha and pines in the forest surrounding these openings were thinned; (3) mix of treatments (1791 ha) including single-tree selection, group selection, seed-tree cuts, and unharvested areas in stands of approximately 18 ha; and (4) unharvested forest (836 ha) consisting mostly of mature, second-growth pine-hardwood forest. Partially harvested and group selection areas retained unharvested buffer strips (greenbelts) along ephemeral stream drains. These greenbelts were primarily second-growth forests of mixed pine-hardwood or hardwood (≥50 years old) and were approximately 15–50 m wide. Throughout the basin, unharvested stands and stands in various stages of regeneration were interspersed within the treatment units. Consequently, with the treatment units, unharvested areas, and industrial timberlands, the Winona Basin contained most of the predominant forest types, seral stages, and forest management practices that existed in the Ouachita Mountains.

2.2. Bat capture and radiotelemetry

From 2000 to 2005, we captured bats between 2100 and 0130 CST using 3–8 mist nets (2.6–12.0 m wide × 2.6 m tall) at 21 trapping areas distributed throughout the basin. Trapping locations were primarily stream pools, but also included forest roads, culverts, bridges, ponds, and dry creek beds. We recorded age (juvenile or adult), sex, and reproductive condition of all individuals captured. We followed the guidelines of the American Society of Mammalogists for capture, handling, and care of mammals (Animal Care and Use Committee, 1998).

We used radio transmitters to locate bats at their diurnal roost sites from mid-May until early August (summer henceforth). We bonded transmitters to the mid-scapular region with surgical adhesive following partial hair removal. Transmitters weighed either 0.32 or 0.70 g and were equipped with 10- or 21-day batteries, respectively. Transmitter load was 2.6–8.4% of body weight and averaged 4.5% (±0.5 S.E.). We radiotracked each bat to its roost site the morning following capture and approximately 5 days/week thereafter. When bats could not be visually confirmed in the roost via binoculars, tree climbing, or exit counts, we collected habitat data surrounding the roost site, but did not collect data specific to the roost tree (e.g., tree species). We estimated number of bats in each roost either visually or by conducting exit counts at dusk.

2.3. Roost and site characterization

For visually confirmed roosts, we recorded tree species and diameter at breast height (dbh). We measured roost height and total tree height with a clinometer. We characterized habitat surrounding each roost in a 17.84-m radius (0.1-ha) plot centered on the roost tree. For roosts that lacked visual confirmation, this plot was centered on the general area indicated by radiotelemetry. Within the plot, all woody stems >1 m tall and <5 cm dbh were counted, and all woody stems >1 m tall and ≥5 cm dbh were recorded by dbh and species. We measured diameters of all snags (by pine or hardwood) ≥5 cm dbh within the plot. We measured canopy cover at four locations (90° apart) along the outer edge of each plot using a spherical densitometer and averaged these measures for the plot.

To determine site characteristics that may have affected roost selection, we selected random sites to compare with roost plots. Identical habitat measurements were collected for random and roost plots. To ensure random plots were available to bats, we selected a random tree or snag (depending on the roost substrate) for each roost tree by choosing the first tree ≥5 cm dbh (hardwood or pine) and >40 m distance, at a random azimuth from the roost location. When adjacent roost locations were ≤20 m apart (n = 2 roosts), we measured a single plot (centered between roosts) and a single corresponding random plot. When ≥2 instrumented bats shared a roost (n = 2), that roost was included in the analyses only once, and randomly assigned to one bat.

2.4. Analysis

We compared roost heights, snag heights, and diameters of snags selected for roosting between males and females using *t*-tests. We compared the proportion of roosts in pine and

Table 1
Vegetative characteristics (from 0.1-ha plots) considered in logistic regression models comparing roost sites of male and female northern long-eared bats with random locations in the Ouachita Mountains of Arkansas, 2000–2005

Variable	Description
Cover	Average overstory canopy cover (%)
Under5	Number of woody stems < 5.0 cm dbh
H5to25	Number of hardwoods 5.0–24.9 cm dbh
Hover25	Number of hardwoods ≥ 25.0 cm dbh
P5to10	Number of pines 5.0–9.9 cm dbh
P10to25	Number of pines 10.0–24.9 cm dbh
Pover25	Number of pines ≥ 25.0 cm dbh
Hsnag<10	Number of hardwood snags < 10.0 cm dbh
Hsnag≥10	Number of hardwood snags ≥ 10.0 cm dbh
Psnag<10	Number of pine snags < 10.0 cm dbh
Psnag≥10	Number of pine snags ≥ 10.0 cm dbh

hardwood snags with the proportion of available snags in random plots using χ^2 goodness-of-fit tests.

We used matched-pairs (each roost matched with its random location) conditional logistic regression (Hosmer and Lemeshow, 2000) to determine habitat parameters surrounding roosts that resulted in 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 habitat parameters (Table 1) derived from 0.1-ha plots surrounding roost and random trees. We 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 χ^2 statistic (SAS Institute Inc., 2000). We determined the most parsimonious model among these candidate models based on the value of Akaike's information criterion (AIC; Burnham and Anderson, 2002) modified for small samples (AIC_c; Anderson et al., 2000). We used multimodel inference by averaging parameter estimates of models within two units of AIC_{min} (Burnham and Anderson, 2002); we used weights (ω_i) calculated among all models within two units of AIC_{min} for averaging and we calculated odds ratios from averaged parameter estimates. Odds ratios were the odds of roost/random. We computed weighted unconditional standard errors for each parameter (Burnham and Anderson, 2002).

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 class. Forest habitat classes were derived from ONF forest stand maps of the study area. Those maps were updated and corrected using a 10-m digital color orthoquad (DOQ) and ground-truthing. We defined available habitat 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) is larger than mean home ranges reported by Menzel et al. (2003) for northern long-eared bats in the Allegany Mountains of West Virginia (range: 43–578 ha; mean = 216 ha), but is similar to mean distance between trap site and first roost (1001 m) reported

for female northern long-eared bats in New Brunswick (Broders et al., 2006).

For site-level models and roost tree comparisons (e.g., roost height, roost tree diameter), individual bats were the experimental unit; we calculated mean parameters for each individual and used these means as the experimental unit. Roosts were the experimental unit for analyses using χ^2 tests (comparisons of pine and hardwood snag use and availability).

3. Results

We tracked 17 adult males to 43-day roosts (40 visually confirmed) and 21 adult and 2 juvenile females to 49-day roosts (42 visually confirmed). Females roosted alone (31% of roosts) and in colonies (69%). Colonies ranged from 2 to 51 bats. For colonies with >2 individuals, average colony size was 17.8. Visual observations and exit counts indicated adult males roosted alone. Most bats switched roosts during the study and some maternity colonies moved among snags that were aggregated in a relatively small area (<2 ha). Occasionally, instrumented bats roosted together in large colonies, but then roosted in adjacent smaller colonies on subsequent nights.

Roosts were located under loose bark, in cavities, and in crevices of snags (90%) and live trees (10%; Table 2). For males, 60% of roosts were under loose bark, 25% in cavities, and 15% in crevices. For females, 43% of roosts were under loose bark, 14% were in cavities, and 43% were in crevices. Males tended to roost more in live trees (15% of roosts) than females (5%; Table 2). Shortleaf pine was the most utilized tree species (71% of all roosts). Most (67%) roosts were in shortleaf pine snags. Based on availability of snags ≥10 cm dbh (48.6% pine and 51.4% hardwood), both sexes preferred pine snags over hardwood snags (males: $\chi^2 = 14.47$, d.f. = 1, $P < 0.001$; females: $\chi^2 = 17.47$, d.f. = 1, $P < 0.001$).

In shortleaf pine snags, the two most common types of roosts were under large (generally >30 cm × 30 cm) pieces of exfoliating bark and in long (>1 m) cracks or splits at the top of broken snags. Exfoliating bark roosts were closed at the top and open below; thus, they provided shelter from rain and space for many bats. Roosts in splits (crevices) were open at the

Table 2
Number of snags and live trees of eight species used for roosting[a] by male and female northern long-eared bats in the Ouachita Mountains of Arkansas, 2000–2005

Tree species	Male		Female	
	Snag	Live	Snag	Live
Pinus echinata	23	2	32	1
Quercus alba	5		3	
Acer rubrum	3	2	3	
Q. falcata	1		1	
Q. velutina	1	2		
Q. rubrum			1	
Nyssa sylvatica	1			
Prunus serotina				1
All species	34	6	40	2

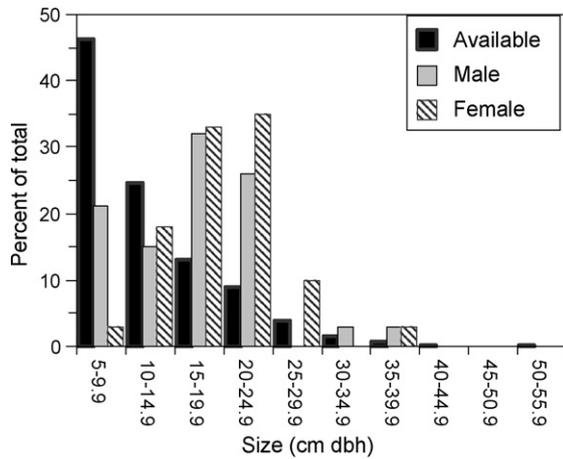[a] Includes only visually confirmed roosts.

Fig. 1. Size distribution (cm dbh) of available snags ≥ 5 cm and distribution of snags used by male and female northern long-eared bats in the Ouachita Mountains of Arkansas, 2000–2005. Mean diameter of snags used for roosting was 15.6 cm for males and 19.1 cm for females.

top and were created when the tops of pines were broken off while the trees were still living.

Mean snag height used for roosting (male = 7.9 m $\pm$ 0.7 S.E.; female = 8.7 m $\pm$ 0.6) did not differ between sexes ($t = 0.85$; d.f. = 35; $P = 0.401$), nor did roost height (male = 4.9 m $\pm$ 0.6 S.E.; female = 5.2 m $\pm$ 0.5; $t = 0.42$; d.f. = 35; $P = 0.679$). However, mean dbh of snags used by females (18.7 cm $\pm$ 1.0) was significantly greater than snags used by males (15.0 cm $\pm$ 1.3; $t = 2.21$; d.f. = 35; $P = 0.034$). Although 91% of snags used for roosting by both sexes were >10.0 cm dbh, most (80%) were 10–24.9 cm dbh (Fig. 1). Size distribution of snags used by males was bimodal; males tended to roosts in small understory snags (<10 cm) more than females (21% of male roosts versus 2% of female roosts). Seven male roosts (two in red maple [*Acer rubrum*], four in oaks, and one in a blackgum [*Nyssa sylvatica*]) were located in cavities of small snags (<10 cm) in the understory, whereas only one female roost was located in a small understory red maple snag.

For females, logistic regression differentiating roost sites from random sites included four models within two units of AIC_{min} (Table 3). The parameter-averaged model for females included the following variables: Hover25 (estimate = -0.576 $\pm$ 0.275 S.E.; odds ratio = 0.562), Psnag<10 (estimate = 0.087 $\pm$ 0.067; odds ratio = 1.091), Pover25 (estimate = 0.139 $\pm$ 0.146; odds ratio = 1.149), P5to10 (estimate = $-0.186 \pm$ 0.147; odds ratio = 0.829), and Hsnag<10 (estimate = -0.059 $\pm$ 0.052; odds ratio = 0.942). Females were more likely to roost at sites with more large overstory pines (Pover25), more small pine snags (Psnag<10), fewer midstory pines (P5to10), fewer understory hardwood snags (Hsnag<10), and fewer large overstory hardwoods (Hover25) than random. For males, logistic regression analyses differentiating roost sites from random sites included three models within two units of AIC_{min} (Table 3). The parameter-averaged model for males included the following variables: Pover25 (estimate = 0.196 $\pm$ 0.137 S.E.; odds ratio = 1.217), P10to25 (estimate = $-0.068 \pm$ 0.058; odds ratio = 0.934), and Psnag$\geq$10 (estimate = 0.083 $\pm$ 0.087; odds ratio = 1.087). Males were more likely to roost at sites with more large overstory pines (Pover25) and overstory pine snags (Psnag$\geq$10), and fewer relatively small overstory pines (P10to25) than random.

Direct comparisons (t-tests) of vegetation surrounding roost sites suggested the primary difference between male and female roost locations was abundance of midstory trees. Number of midstory trees (5–9.9 cm dbh) in 17.84-m plots surrounding female roost sites (16.0 $\pm$ 2.7 S.E.) was significantly lower than at male roost sites (29.9 $\pm$ 4.4; $t = -2.84$; $P = 0.007$). Further, mean number of small overstory trees 10–24.9 cm dbh surrounding female roosts sites (24.6 $\pm$ 3.3) was 73% of numbers surrounding male roost sites (33.8 $\pm$ 3.8), but this difference was not significant ($t = -1.84$, $P = 0.074$). Thus, density of midstory and small overstory trees was generally lower at female roost sites. Although mean canopy cover at male roost sites (74.5% $\pm$ 3.4 S.E.) was greater than at female roosts sites (66.0% $\pm$ 3.8), the difference was not significant ($t = -1.60$, $P = 0.117$).

Roosts were located in eight forest classes, but 89% of all roosts were located in three classes (Table 4). Stands that were

Table 3
Variables included, values of AIC_c, difference from AIC_{min} (Δ_i), model weights (ω_i), and maximum-rescaled R^2 for sex-specific models within two units of AIC_{min} comparing roost sites of northern long-eared bats and random locations in the Ouachita Mountains of Arkansas, 2000–2005

Model	AIC_c	Δ_i	ω_i	R^2
Females[a]				
−Hover25	27.659	0.000	0.416	0.22
−Hover25 + Psnag<10	28.805	1.146	0.235	0.27
−Hover25 + Pover25 − P5to10	29.391	1.732	0.175	0.35
−Hover25 + Pover25 − P5to10 − Hsnag<10	29.415	1.756	0.173	0.46
Males[a]				
+Pover25	21.362	0.000	0.430	0.18
+Pover25 − P10to25	21.936	0.574	0.322	0.30
+Pover25 − P10to25 + Psnag≥10	22.471	1.109	0.247	0.43

Model parameters are defined in Table 1. (+) Positive association with roost location in model and (−) negative association in model.

[a] Because of missing data, $n = 22$ female bats and 16 male bats.

Table 4
Number (percent in parenthesis) of roosts in nine forest classes used by male and female northern long-eared bats and percent availability of each class (based on merged 1000-m radius circles surrounding each roost) in the Ouachita Mountains of Arkansas, 2000–2005

Habitat	Males	Females	Available (%)
P/H[a] partially harvested/thinned	14 (33)	27 (55)	21
Unharvested P/H 50–99 years old	12 (28)	11 (22)	22
P/H group selection	9 (21)	9 (18)	16
Unharvested hardwood 50–99 years old	3 (7)	1 (2)	10
Unharvested P/H > 100 years old	3 (7)		4
P/H 30–49 years old		1 (2)	2
Closed-canopy loblolly plantation	1 (2)		10
Older/thinned loblolly plantation	1 (2)		3
Other habitats			12
All habitats	43	49	

[a] Mixed pine-hardwood forest.

partially harvested or thinned with partial midstory (trees <15 cm dbh) removal was the most used forest class, and 55% of female roosts were located in this forest type. Twenty percent of all roosts were located in group selection stands and 25% were located in unharvested, second-growth forests of mixed pine-hardwood. More male roosts (42%) were in unharvested stands than female roosts (24%).

4. Discussion

Most previous roosting studies have emphasized the importance of hardwoods for roosting by northern long-eared bats (e.g., Sasse and Pekins, 1996; Foster and Kurta, 1999; Menzel et al., 2002; Owen et al., 2002; Jackson, 2004; Carter and Feldhamer, 2005; Ford et al., 2006). However, in forests of New Brunswick that contained both deciduous and coniferous stands, female northern long-eared bats roosted primarily in hardwoods whereas males roosted mostly in conifers (primarily red spruce [*Picea rubens*]; Broders and Forbes, 2004). In mixed forests of northeastern Kentucky, 30% of northern long-eared bat roosts (both sexes combined) were in shortleaf pines (Lacki and Schwierjohann, 2001). Our results indicate that in mixed pine-hardwood forests of Arkansas, pine snags are used extensively by both male and female northern long-eared bats and are preferred by both sexes over hardwood snags. Although the geographic range of northern long-eared bats does not encompass large areas dominated by shortleaf pine, our results indicate that shortleaf pine snags are important to the roosting ecology of this species on the southern edge of its range.

In previous studies of northern long-eared bats, live trees comprised an average 37.0% (±6.3 S.E.; range 17–63%) of roosts (Sasse and Pekins, 1996; Foster and Kurta, 1999; Lacki and Schwierjohann, 2001; Menzel et al., 2002; Jackson, 2004; Carter and Feldhamer, 2005; Ford et al., 2006), versus only 10% in our study. This lower use of live trees may reflect a greater availability of snags compared with other studies. Many of the pine snags used for roosting were created by an ice storm during winter 2000. Pines located in thinned areas accumulated heavy loads of ice during this event, resulting in many broken tops and subsequent tree deaths. Based on a random sample, approximately 50% of roost snags bore evidence of creation by that ice storm and no other large-scale wind event occurred during this period that could account for the damage these trees sustained.

Reasons why northern long-eared bats preferred pine snags over hardwood snags are unknown. Because many pine snags were created during the 2000 ice storm, most still retained large sheets of exfoliating bark that provided favorable roosting conditions for large groups of bats. Further, long cracks (>1 m) at the tops of pines, created when tops of live trees were broken, provided ample space for many bats and 39% of female roosts were in these locations. However, as these snags age, exfoliating bark will eventually fall off, making them unusable, whereas the cracks will likely remain substantially longer. Consequently, snags in a variety of age classes are important to ensure a sustainable supply of adequate roosting sites.

Males roosted in snags with significantly smaller diameter than females and males frequently roosted in cavities of small (<10 cm) trees. Similarly, Lacki and Schwierjohann (2001) found males frequently roosted in small diameter (mean = 14.4 cm dbh) trees and Broders and Forbes (2004) found males frequently roosted in trees <20 cm dbh. In our study, males more readily used these abundant small snags, suggesting males are more flexible than females in their selection of roost trees.

The fission–fusion model suggests that colonies of some bats may consist of multiple roosting subgroups, spread among different trees within the roosting area (Kerth and König, 1999). During roost switching, subgroups break apart and mix. We found large maternity colonies dispersed to multiple trees in a relatively small areas (generally <2 ha) surrounding the original colony, but in all cases, subsequent roosts contained smaller groups of bats. For example, 1 female roosted with >30 individuals on day 1, 10 bats on day 2, and 3 bats on day 5. However, this dispersion may have resulted from predator avoidance because the original roost containing >30 individuals was abandoned on night 2 and a black rat snake (*Elaphe obsoleta obsoleta*) was observed descending from the snag during the exit count that night. Nevertheless, colony size of northern long-eared bats has been found to decline during the reproductive period from pregnancy through post-lactation (Sasse and Pekins, 1996; Foster and Kurta, 1999; Lacki and Schwierjohann, 2001).

More roosts of female northern long-eared bats were in partially harvested and group-selection stands than male roosts (73% of female roosts versus 53% of male roosts). Further, in these stands, females roosted less in unharvested greenbelts surrounding stream drains than males (29% of female roosts versus 48% of male roosts; Perry et al., 2007). Thus, females tended to roost in more open forest conditions than males. Most (69%) female roosts were colonies that contained young. Roost trees located in more open habitats may receive greater solar radiation, which may speed development of young (Racey and Swift, 1981; Vonhof, 1996), and Kerth et al. (2001) found female tree-roosting bats select warmer roosts during parturition. We found canopy cover was generally lower at female roosts than male roosts but the difference was not significant. However, mean number of midstory trees surrounding female roost sites was approximately half that of male roost sites. Constantine (1966) suggested that roosts of female *Lasiurus* bats were located high in trees, which permitted young bats a greater opportunity to conduct successful initial flights. Similarly, maternity roosts of northern long-eared bats that are located in areas with few midstory trees may provide more open areas immediately around and below roosts that would otherwise impede inexperienced juvenile flyers.

Our models comparing vegetation surrounding roost sites with random locations indicated female roost sites were more likely to have more large overstory pines ≥25 cm dbh, fewer large overstory hardwoods, fewer midstory pines (5–9.9 cm), fewer small (<10 cm dbh) hardwood snags, and more small pine snags than random. These parameters are reflective of conditions in partially harvested, pine-dominated stands where 55% of female roosts occurred. In these areas, most midstory (<15 cm dbh) trees were removed and densities of overstory

hardwoods were reduced. Other studies have found roost sites of mostly female northern long-eared bats had greater mean stand dbh (Sasse and Pekins, 1996; Lacki and Schwierjohann, 2001) and had greater numbers of overstory trees (Owen et al., 2002) than random sites, which (similar to our results) suggests roosts were associated with stands dominated by mature, overstory trees. However, we found females roosted mostly in stands where overall numbers of mature overstory trees (especially hardwoods) were reduced through partial harvest.

Although Broders and Forbes (2004) suggested that timber harvest may have a significant negative effect on female northern long-eared bats, we found that most female roosts were in areas that had undergone partial harvesting and midstory reduction/removal; this occurred despite readily available (32% of available habitat) unharvested, second-growth stands in our study area. Similar to our results, Menzel et al. (2002) found all roosts of maternal female northern long-eared bats were in stands that had undergone recent (<10 years) diameter-limit (40 cm dbh) cutting, and understory vegetation density (woody vegetation <9.5 cm dbh) was less at roost sites than random sites.

Ford et al. (2006) found all roosts of male northern long-eared bats in unmanaged, mature, second-growth forests, whereas we found 35% of male roosts in those forest classes (unharvested 50–99-year-old stands). However, we found 47% of all male roosts in unharvested stands (including stands ≥100 years old) and 48% of male roosts in partially harvested stands were in unharvested greenbelts (67% of all male roosts were unharvested sites versus 45% of female roosts), suggesting males may prefer more dense stands for roosting. Our models differentiating male roost sites from random sites suggested that males were more likely to select sites with abundant large (≥25 cm dbh) overstory pines, fewer small overstory pines (10–24.9 cm dbh), and more large pine snags ≥10 cm dbh.

Differences in model parameters between males and females likely resulted from males tending to roost more in unharvested stands, unharvested greenbelts, and group-selection stands (where larger overstory pines dominated) than females (Table 4). In New Brunswick, male northern long-eared bats roosted primarily in conifer-dominated stands, whereas females roosted more in deciduous stands (Broders and Forbes, 2004). However, our results indicated both sexes roosted mostly in pine-dominated, mixed pine-hardwood stands where pine snags were abundant. Using Euclidean distance analysis, Perry et al. (2007) found both male and female northern long-eared bats preferred to roost in or in close proximity to thinned mature (>50 years old) stands of mixed pine-hardwood.

5. Conclusion

In the Ouachita Mountains, both sexes of northern long-eared bats roosted primarily in snags, both sexes preferred pine snags over hardwood snags, and females roosted in snags that were greater in diameter and surrounded by fewer midstory trees than males. More specifically, pine snags ≥10 cm dbh, located in areas of relatively open forests (approximately 15 m²/ha of overstory trees with a reduced or removed

midstory), appear to be an important habitat component for female northern long-eared bats during summer in the Ouachita Mountains. Furthermore, males appear more flexible than females regarding snag size. Both sexes readily roosted in partially harvested stands that were subjected to midstory removal and burning where snags created by an ice storm in 2000 were abundant. Abundance of pine snags ≥10 cm was likely not a limiting factor for northern long-eared bats in our study area because pine snag densities (from random plots) throughout the study area averaged 42.3 snags/ha ± 4.5 S.E., and densities of all snags ≥10 cm dbh was 82.0 ± 6.0 snags/ha. In the absence of large-scale disturbances such as the ice storm that occurred in our study area, long-term sustainability of overstory pine snags in areas of reduced overstory BA is unknown and warrants further study. Although managers frequently create and retain hardwood snags because of their perceived greater longevity compared with pine snags, abundance of pine snags created either naturally or via management, may warrant consideration in management for this species.

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