Winter Roosting Ecology of Silver-haired Bats in an Arkansas Forest

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Abstract - Although summer roosting by *Lasionycteris noctivagans* (Silver-haired Bats) has been studied in various ecological regions of North America, no quantitative studies have examined winter roost selection. We radiotracked 11 bats to 31 day-roosts during winter in forests of the Ouachita Mountains, AR. We quantified roost structures and examined the association between roosts and forest stands. We also examined effects of temperature on roost use. Ninety percent of roosts were in trees (5 species): 55% of all roosts were under loose bark on the bole of live overstory *Pinus echinata* (Shortleaf Pine), 3% of roosts were in a rock outcrop, and 6% were at ground level (under a tree root or in a cavity at the base of a live pine). Bats selected pine or pine-hardwoods stands >50 years old, and used forest stands 15–50 years of age less than their availability. Roost locations were influenced by temperature and solar radiation; most (90%) roosts were on southern topographic aspects, and bats roosted in the rock outcrop or on the ground on colder days (<5 °C). Retaining open pine and hardwood stands >50 years old on south slopes would likely maintain roosting habitat for wintering Silver-haired Bats in the Ouachita Mountains.

Introduction

For bats, roost sites are critical for hibernation, rearing young, protection from predators, and thermoregulation (Kunz and Lumsden 2003). Because roosts are critical to survival of forest bats (Vonhof and Barclay 1996), an abundance of studies on roost selection in forested ecosystems has recently emerged (e.g., Kalcounis-Rüppell et al. 2005). Despite recent gains in understanding the summer roosting ecology by temperate forest-dwelling bats, information on roosting ecology during winter is limited (Cryan and Veilleux 2007).

Many bats common in forests during summer migrate to other areas or move short distances to hibernate in caves, mines, or man-made structures during winter (Kunz and Fenton 2003). Only a few bats that inhabit temperate regions are known to roost in trees during winter (Cryan and Veilleux 2007), and the extent that these bats hibernate is unknown. Instead, these bats arouse to forage during warm winter nights and undergo bouts of torpor to limit energy expenditure during unfavorable conditions (i.e., below freezing temperatures). This behavior is common in foliage-roosting bats (genus *Lasiurus*), which often roost in leaf litter during winter (Hein et al. 2005,

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Mormann and Robbins 2007, Saugey et al. 1998). During winter, roosting bats experience different physiological and survival pressures from those of summer. Furthermore, mortality among tree bats during winter may be high (Cryan and Veilleux 2007). Thus, roost sites selected by tree bats during winter may be especially important to their survival.

Lasionycteris noctivagans LeConte (Silver-haired Bat) occur throughout North America, from southern Alaska and central Canada to northern Mexico (Kunz 1982), and are considered a migratory species. During winter, Silver-haired Bats migrate to the southern United States and generally reside south of a line from Pennsylvania to Missouri to southern Arizona and California (Izor 1979). They are generally absent in the southeastern United States during summer (June–August; Cryan 2003). During migration and summer residency, female Silver-haired Bats either roost alone or in maternity colonies, whereas males typically roost alone (e.g., Barclay et al. 1988, Betts 1998, Mattson et al. 1996). During winter, Silver-haired Bats roost in mines, caves, houses, rock crevices, under loose bark, and in hollow trees (Beer 1956, Frum 1953, Jackson 1961, Pearson 1962). Although Silver-haired Bats may hibernate in caves in northern portions of their winter range, they may remain active during winter in southern portions (Izor 1979). Other than anecdotal accounts of winter roosts, little is known about their roosting ecology in forests during winter. Therefore, our objective was to quantify characteristics of roosts used by Silver-haired Bats during winter in forests of Arkansas. Using radiotelemetry, we examined the types of roost structures used, the types of forest habitats where roosts were located, and the effects of ambient temperature on roost locations.

Study Area

We conducted the study on the Jessieville Ranger District of the Ouachita National Forest (ONF), in southern Perry and northern Garland counties (34°45'N, 93°15'W), within the Ouachita Mountains of central Arkansas. The Ouachita Mountains consist of east–west oriented mountains and valleys that extend from central Arkansas into east-central Oklahoma. Elevations in the region range from 100 m to 800 m, mean annual precipitation ranged from 112 cm to 142 cm, and the growing season was 200–240 days (McNab and Avers 1994). Winters are generally mild. During our study, average maximum temperature from December to March in the area was 12.4 °C and average minimum temperature was -2.1 °C, although the temperature occasionally fell below -12.0 °C; average monthly precipitation was 10.0 cm, with 1.3 cm of this being frozen precipitation (NOAA 2009).

The 9619-ha study area was >99% forested, with <1% agricultural lands. The most abundant forest type (43%) in the study area was mixed *Pinus echinata* P. Mill (Shortleaf Pine)-hardwood forests managed by ONF. The hardwood component in these forests was diverse (>32 species) and was primarily *Quercus* spp. (oaks), *Carya* spp. (hickories), and *Acer rubrum* L. (Red Maple). The study area also contained forests of mostly pure Shortleaf Pine

(35%) and oak-hickory forest (14%). Nine percent of the area was intensively managed, private timberlands that consisted mostly of closed-canopy *P. taeda* L. (Loblolly Pine) plantations of approximately 20 years of age.

Methods

We captured bats between 1900 and 2200 CST with mist nets placed across the North Fork of the Ouachita River, from 1993 to 1996. We determined bat sex and weighed and banded captured bats, but did not determine the ages of bats (juvenile or adult) because bats were captured after ossification of metacarpal-phalanx joints (Racey 1974). We attached 0.71-g radiotransmitters (Holohil Systems Limited, Carp, ON, Canada) to the midscapular region with Skin Bond® surgical adhesive (Smith and Nephew, Inc., Largo, FL). In addition, we instrumented 2 bats from a colony we found in a rock outcrop via radiotelemetry. Mass of all captured males averaged 11.3 g, and mass of females averaged 12.2 g (range = 10.3–13.8 g); transmitter mass was 5.1–6.9% of bat mass and averaged 6.0 ± 0.2%. From 11 December to 19 March, 1993–1996, we tracked instrumented bats to their roosts daily (with a few exceptions) until transmitter batteries failed or the radio signal could no longer be located. Because of the relatively low heights of roosts in trees, we visually located bats from the ground in all but 1 roost. Our methods of capture, handling, and care of bats adhered to guidelines of the American Society of Mammalogists (Gannon et al. 2007).

At each tree roost, we recorded tree species, diameter at breast height (dbh; cm), aspect (N, S, E, or W) of roost on tree, and height (m) of the bat in the roost using a clinometer. We also recorded topographic aspect (N, S, E, or W) of each site using a compass. Our primary interest was in responses by the species, and not sex-specific differences in roost selection. Furthermore, we found no difference between males and females in diameter of trees used (t_{26} = 0.90, P = 0.377), heights of roosts in trees (t_{29} = –2.00, P = 0.060), or proportions of habitats used (χ^2 = 3.85, df = 2, P = 0.146). Therefore, we combined data for males and females for all analysis. We present all means ± SE.

To determine habitat selection among types of forests stands, we delineated 6 forest classes using digital maps and forest-stand information obtained from ONF; these maps included forest types, stand ages, and management history. We determined locations of bat roosts across the study area either from global positioning system coordinates or estimated locations on topographic maps. We overlaid roost locations on vegetation maps in a geographic information system and determined proportion of roosts in each forest class. To determine available habitat, we created a 1169-m-radius buffer around each roost. The radius of these buffers was based on mean distance from capture site to roost locations for radiotracked bats (1169 ± 259 m). We combined all buffers into a single polygon and designated this area the available habitat; we then determined the percent of available habitat comprised by each forest class. We compared proportion of used habitat types to proportion of available habitat types with multiple binomial tests. We used the Benjamini-Hochberg method to control the positive false discovery rate (FDR) for the overall experiment at 0.05 (Benjamini and Hochberg 1995, Waite and Campbell 2006). We included each roost only once, regardless of the number of times the roost was used, in analyses of spatial location (e.g., forest-stand use) and roost characterizations (e.g., roost aspect, roost height).

To determine if temperature affected roost placement, we obtained regional weather data (minimum and maximum daily temperatures) from the National Weather Service (NOAA 2009). We used weather data from the closest weather station (Blakely Mountain Dam), which was approximately 21 km from the study site. We used a *t*-test to compare mean minimum daily temperature when roosts were located in trees with the mean temperature when roosts were located in rock crevices or at ground-level.

Results

We captured and instrumented 13 bats (10 females and 3 males); however, 2 females were not relocated. Maximum temperature of days when bats were captured using mist nets averaged 15.6 ± 1.4 °C (range = 6.1–20.0 °C), and minimum daily temperature averaged -1.6 ± 1.7 °C (range = -6.1–8.9 °C). Generally, bats were captured on days when the average temperature was >4.0 °C.

For the 11 bats we located via radiotelemetry, each bat was found an average of 14.4 days (range = 5–26 days). We documented 31 roosts (22 for females and 9 for males). The mean number of roosts located for each bat was 3.0 ± 0.6 (range = 1–6), and the mean number of days we found a bat in a particular roost was 5.1 ± 0.9 (range = 1–20). One bat was tracked to a Shortleaf Pine, but its location in that tree was not determined, and the location within the study area of another roost was not recorded.

Twenty-eight roosts were in trees, 1 roost was in a crack of a rock outcrop, and 2 roosts were on the ground. The rock outcrop was used by 3 instrumented female bats during different tracking periods. Other non-banded bats were periodically observed in the rock crevice, indicating the outcrop was used by multiple bats over multiple years and occasionally contained small colonies of 2–3 bats. Of the 2 roosts on the ground, one was located in a hole at the base of a tree, and one was located under an exposed root.

Most (74%, *n* = 23) roosts were in Shortleaf Pine. Other tree species used for roosting were *Nyssa sylvatica* L. (Blackgum; 3%, *n* = 1), *Quercus rubra* L. (Northern Red Oak 3%, *n* = 1), *Quercus alba* L. (White Oak; 10%, *n* = 3), and under the roots of a Red Maple (3%, *n* = 1). Average diameter at breast height (dbh) of all roost trees was 33.1 ± 2.0 cm (range = 10.2–50.8 cm). In trees, the average height to roost was 5.1 ± 0.5 m (range = 1.0–9.1 m). Among all roosts that were visually confirmed, 57% (*n* = 17) were under loose bark on the bole of live overstory Shortleaf Pines (mean tree dbh = 31.8 ± 2.5, range = 10.2–49.8 cm). Five roosts (17%) were in cavities of live hardwoods (mean tree dbh = 41.3 ± 3.3, range = 31.2–50.8 cm), including 1 roost in a basal cavity of a large (43.9 cm dbh) Blackgum. One roost (3%) was in a crevice of a Shortleaf Pine that was created by a lightening strike. Four roosts (13%) were on the boles of Shortleaf Pines, where the bat was found in sunny spots without cover. Most roosts located under loose bark of tree boles were on southerly sides of trees; aspect of bats on the boles were 14% north facing (n = 3), 5% east facing (n = 1), 5% west facing (n = 1), and 76% (n = 16) southerly (90°–270°). Bats disproportionally located their roosts on south-facing aspects; 3% were east facing (n = 1), 7% were north facing(n = 2), and 90% (n = 27) were on southerly aspects (90°–270°; Fig. 1).

Bats switched between tree roosts and roosts located in the rock outcrop or on the ground (in holes or under tree roots). Use of these rock and ground roosts appeared to be influenced by minimum ambient temperatures. The mean minimum temperature of days when instrumented bats roosted in the rock outcrop or on the ground (-5.6 ± 1.1 °C) was significantly less

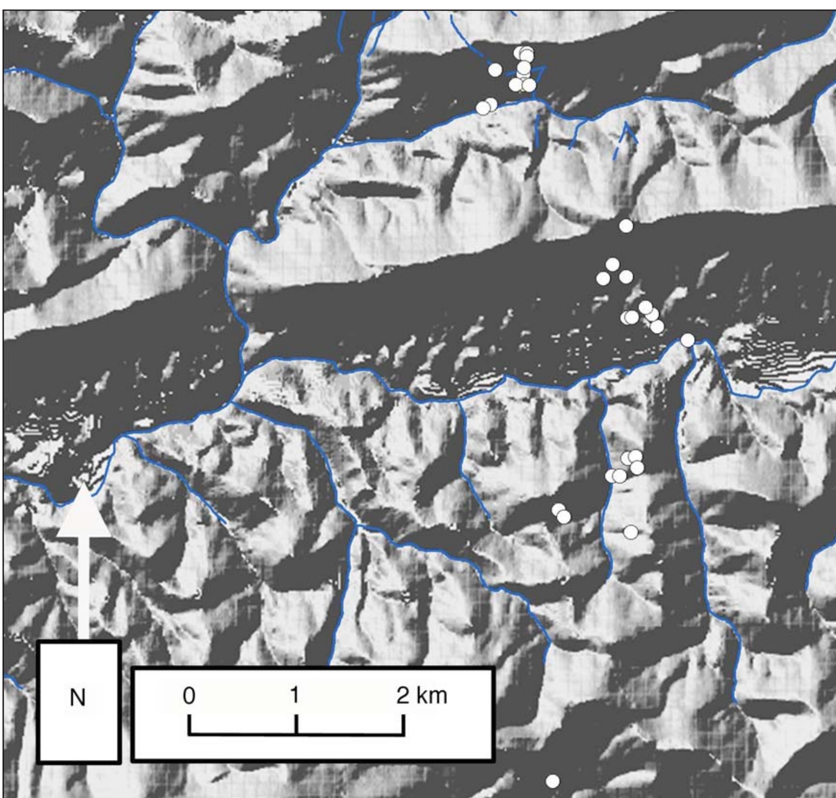

Figure 1. Locations of winter roosts (n = 30) used by Silver-haired Bats in relation to topography and aspect in the Ouachita Mountains of Arkansas. Dark areas represent areas of southern and southeastern aspect; lighter areas are northern and western aspects. Roost locations are represented by white circles.

(t_{171} = -3.82, P = 0.002) than days when roosts were located in trees (-0.5 ± 0.4 °C). In general, bats tended to use the rock and ground roosts more often when temperatures fell below -4 °C (Fig. 2).

Silver-haired Bats roosted in 4 forest classes (Table 1). Among the 6 forest classes for which we compared use with availability, bats selected pine or pine-hardwood stands >50 years old. They also selected pine or pine-hardwood stands >50 years old that had recently been partially harvested

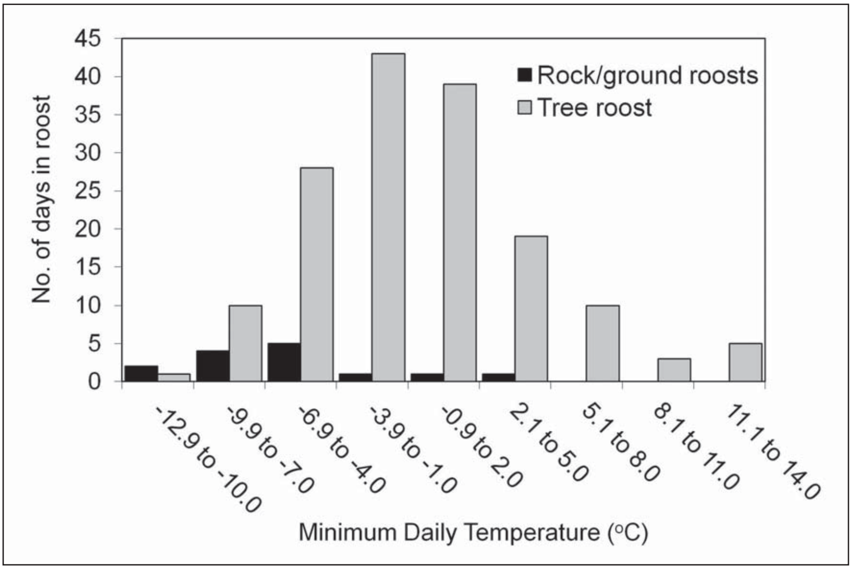

Figure 2. Minimum daily temperature (°C) and total number of days Silver-haired Bats roosted in 2 types of roosts during winter in the Ouachita Mountains of Arkansas. Tree roosts were located under bark, in cavities, or in crevices above ground in standing trees. Rock and ground roosts were either in the crevice of a rock outcrop or on the ground (in holes or under tree roots).

Table 1. Proportions of available forest classes (derived from merged 1169-m radii around roosts) compared with proportions of habitats used for roosting by Silver-haired Bats (n = 30 roosts) during winter in the Ouachita Mountains of Arkansas.

Forest class	Available %	Used % (no. roosts)	Z	P^A	Select or avoid
<15 years old, P[B] or P/H	9.6	3.3 (1)	–1.17	0.244	
15–50 years old, P, H, or P/H[C]	20.4	0.0 (0)	–2.77	0.006*	A
>50 years old, P or P/H	52.2	80.0 (24)	3.05	0.002*	S
>50 years old, H	14.0	3.3 (1)	–1.68	0.092	
>50 years old, P or P/H, partial harvest, burn	3.4	13.3 (4)	3.00	0.003*	S
Others	0.4	0.0 (0)	–0.35	0.728	

[A]Compared using multiple binomial tests and a Z approximation.
[B]For forest types, P = pine, H = hardwood, and P/H = mixed pine and hardwood forests.
[C]Included closed-canopy Loblolly Pine plantations (5.5 % of available).
*Significant difference between used and available; controlled for experiment-wise error rate using Benjamini-Hochberg control of the false discovery rate (FDR).

via single-tree selection and subjected to recent controlled burning. Stands 15–50 years old were used less than their availability, and other habitat types were selected in proportion to their availability. The single roost located in a forest stand <15 years old was the rock outcrop. This outcrop was located in a young clearcut where the rocks were exposed to full sun during the day.

Discussion

We found Silver-haired Bats roosted mostly under loose bark of live, mature (>50 years old) Shortleaf Pines during winter, but they also roosted in other living trees, including cavities of hardwoods. We found no roosts in snags. Similarly, Silver-haired Bats during migration roosted primarily under bark of live *Salix amygdaloides* Anderss (Peach-leaved Willow) in Manitoba (Barclay et al. 1988). We found bats occasionally roosted in cavities that were on the ground, and they roosted relatively low in trees (average height = 5.1 m) compared with studies of summer roost selection (e.g., Campbell et al. 1996, Mattson et al. 1996). In other regions of North America, female Silver-haired Bats (and many other cavity-roosting bats) typically roost in tall snags during summer, which are generally taller than surrounding trees or have less canopy cover than random trees (e.g., Betts 1998, Campbell et al. 1996, Mattson et al. 1996). Roosting in taller, more-exposed trees may increase solar radiation (i.e., heating) that may increase juvenile growth, make roosts more easily accessible, and provide clear areas for navigation by newly volant young. However, roost height of solitary Silver-haired Bats (mostly males) may be lower in height than females in summer (Mattson et al. 1996).

In our study, bats roosted at relatively low heights that provided potential solar exposure. Because deciduous trees comprised ≈40% of all overstory trees and nearly all midstory trees in most stands where bats roosted, abundant sunlight likely reached the forest understory in winter. Roosting low in trees or on the ground during winter appears to be common among some temperate forest bats that roost in forests during winter, including *Lasiurus borealis* Müller (Eastern Red Bats; Mormann and Robbins 2007) and *L. seminolus* Rhoads (Seminole Bats; Hein et al. 2005, 2008). These species often roost in leaf litter when temperatures are coldest (Hein et al. 2005, Mormann and Robbins 2007, Saugey et al. 1998). Although we found Silver-haired Bats did not roost in leaf litter, they occasionally roosted on the ground or in a rock crevice when temperatures were lowest. Roosts also were located primarily on the southern sides of trees that were situated on southern aspects, similar to winter roosts of Eastern Red Bats (Mormann and Robbins 2007). Furthermore, other studies have shown that switching to roosts close to or on the ground during colder periods also may be common among other forest-dwelling bats that remain active during winter (e.g., Boyles et al. 2005, Hein et al. 2008). Roosting on or near the ground during winter likely provides thermal advantages because soil and rocks retain heat during colder days, and ground-level roosts may provide a more thermally stable environment during winter (Boyles et al. 2005, Hein et al. 2008). Thus, ambient temperature and solar radiation appear to be important to the location of roosts during winter, at both the microhabitat scale and topographic landscape scale.

With the exception of one roost located in a rock outcrop in a young clearcut, all roosts were located in pine or pine-hardwood stands that were >50 years old, and bats used stands 15–50 years of age less than available. Older stands provided abundant structure in the form of large, hollow trees and older trees with exfoliating bark. Because young stands typically are more dense (higher stem density) than older stands, these stands were likely more cluttered, which presumably makes aerial navigation more difficult for bats. Furthermore, the dense, closed-canopies of young pine stands likely allow less solar radiation to reach the understory compared with more open, older stands. The extensive use of mature pines we found may have been an artifact related to the topoedaphic response of Shortleaf Pines in the Ouachita Mountains. Shortleaf Pines are shade intolerant and grow primarily on ridge tops and southern slopes in this region where direct sunlight is most available; they are generally not abundant on north slopes. Nevertheless, older stands, with their abundance of roosting sites (i.e., holes or peeling bark on large trees) and more open vegetation structure appeared to be important to the winter roosting ecology of Silver-haired Bats in our study area. Similarly, forests containing mature (>50 years old) trees and less clutter, including thinned and prescribe-burned forests, are important roosting habitats for many species of forest bats during summer, whereas immature forests with dense clutter are generally avoided (e.g., Kalcounis-Rüppell et al. 2005, Perry and Thill 2008, Perry et al. 2007).

Our relatively low sample size and limited geographic spatial scale may have reduced the precision of our inferences. However, this is the first quantitative, telemetry-based study of winter roosting by Silver-haired Bats in the southeastern US. Consequently, we believe our data provides useful insight into the ecology of this species during winter in North America. Because Silver-haired Bats roosted low in overstory trees, mostly on south slopes, and mostly in stands dominated by mature (>50 years old) trees, retaining open pine and hardwood stands >50 years old on south slopes would likely provide suitable roosting habitat for wintering Silver-haired Bats in the Ouachita Mountains.

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