Roost selection by Big Brown Bats in Forests of Arkansas: Importance of Pine Snags and Open Forest Habitats to Males

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Abstract - Although *Eptesicus fuscus* (Big Brown Bat) has been widely studied, information on tree-roosting in forests by males is rare, and little information is available on tree roosting in the southeastern United States. Our objectives were to characterize diurnal summer roosts, primarily for male Big Brown Bats, and to determine relationships between forest structure and roost selection. We quantified 25 male roosts located via radiotelemetry, and describe an additional 9 maternity roosts for females. All roosts for both sexes were in *Pinus echinata* (Shortleaf Pine) snags, and 82% of roost snags were 15–25 cm diameter at breast height (dbh). Most (94%) roosts for both sexes were under loose bark. A logistic regression model differentiating male roost sites from random locations indicated males were more likely to roost in recently thinned, open-forest conditions (less canopy cover, more cut stumps, and fewer understory stems) that contained abundant overstory pines ≥25 cm dbh and abundant snags. Males roosted primarily (84%) in stands that had recently undergone partial harvesting. Maintaining a supply of pine snags ≥15 cm dbh in relatively open forest habitats, including areas undergoing partial harvest, would provide roosting habitat for male Big Brown Bats in the Ouachita Mountains.

Introduction

Unlike most small mammals, maintenance of viable populations of bats requires high adult survival to offset low reproductive rates (Tuttle and Stevenson 1982). Roosts are important to bats, providing protection from predators, thermoregulatory benefits, and places to raise young and interact (Kunz and Lumsden 2003). *Eptesicus fuscus* Beauvois (Big Brown Bat) is a large (14–30 g) insectivorous bat with one of the most widespread mammalian distributions in the Americas, ranging from northwestern Columbia and Venezuela to central Canada (Kurta and Baker 1990). Big Brown Bats roost in a wide variety of structures, including caves and mines (e.g., Beer and Richards 1956, Gates et al. 1984, Mills et al. 1975), rock outcrops (Lausen and Barclay 2006), buildings (e.g., Brigham and Fenton 1986, Whitaker and Gummer 2000), and trees (e.g., Brigham 1991, Kalcounis and Brigham 1998, Rabe et al. 1998).

Because of their widespread distribution, abundance, and propensity for roosting in man-made structures, Big Brown Bats are one of the most widely studied bats in North America (Agosta 2002). However, most studies of roosting behavior have examined roosts in buildings and man-made

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structures, and studies focusing on roosting behavior in forests have been conducted primarily in the western United States and Canada (e.g., Betts 1996, Brigham 1991, Kalcounis and Brigham 1998, Vonhof 1996). Despite being commonly found in forests throughout much of eastern United States (e.g., Lacki and Hutchinson 1999, Mumford and Cope 1964, Saugey et al. 1989, Whitaker 1995), information on roosting in forests of this region is scarce (but see Timpone et al. 2006).

For many cavity-roosting bats that roost in trees during summer, females typically roost in colonies where young are raised, but adult males of these species normally roost alone during the maternity period (e.g., Miles et al. 2006, Perry and Thill 2007). However, previous studies of roosting by bats in forests have focused primarily on females (Hayes 2003). Thus, information on roost selection by males in forests is limited. Females may select roosts that differ from males because of varying selective pressures associated with lactation, space needs, predator avoidance, and thermoregulatory needs (e.g., Hamilton and Barclay 1994, Willis et al. 2006).

Herein, our objectives were to characterize summer diurnal roosts used by adult male Big Brown Bats in a diversely managed forest of Arkansas, and determine relationships between forest structure and roosting. We compared roost trees and surrounding habitat with random locations, and we developed a logistic model relating forest structure to roost selection. Although we concentrate on male roosting, we also present characteristics of 9 roost trees used by females that we located during the study.

Study Area

We conducted the study in the 6545-ha Upper Lake Winona Basin, situated in northwestern Saline County (34º48'N, 92º58'W) in the Ouachita Mountains, AR. 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 100 to 800 m, mean annual precipitation ranges from 112 to 142 cm, mean annual temperature ranges from 16.0 to 17.0 ºC, and the growing season is 200–240 days (McNab and Avers 1994).

The study area contained a diverse assemblage of forest types and management. The area was completely forested; no residential areas, houses, or agricultural lands exist in the study area. Man-made structures within the area consisted of small concrete bridges and drainage culverts. Most (about 63%) of the study area consisted of mixed *Pinus echinata* P. Mill (Shortleaf Pine)-hardwood forests managed by the Forest Service, US Department of Agriculture (Ouachita National Forest [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). Other forest types present in the study area included Shortleaf Pine (about 12%), oak-hickory (about 14%), and riparian forests (trace). Twelve percent (778 ha) of the area was intensively managed industrial timberlands that consisted mostly of closed canopy or older, thinned *P. taeda* L. (Loblolly Pine) plantations. These plantations were typically thinned at about 12–15 years of age and managed on a 30–35 year rotation.

National forest lands within the study area were divided into 6 management blocks (513–1791 ha) where different silvicultural treatments were implemented in 2000. These blocks included pine-woodland restoration (1232 ha), single-tree selection (864 ha), group selection (1044 ha), mixed-management (1791 ha), and a mostly untreated block, which consisted primarily of mature (>50 years old), second-growth pine-hardwood timber (836 ha) (Perry et al. 2007). Stands subjected to timber harvest, including single-tree selection, group selection, and pine woodland restoration areas, retained unharvested buffer strips (greenbelts) along ephemeral drains. These greenbelts were primarily 15- to 50-m wide strips of second-growth forests of mixed pine-hardwood or hardwood (≥ 50 years old). Also throughout the study area, stands (16–90 ha) that were either too steep to manage (e.g., slopes >35%), in regeneration (typically <50 years of age), uneconomical to harvest, or dominated by uneconomical species such as hardwoods, were interspersed within these treatment units.

Methods

Bat capture and radiotelemetry

We captured bats between 2100 and 0130 CDT with mist nets at 10 trapping locations. Trapping locations were mostly small streams, but also included forest trails. We assessed bat age (juvenile or adult) based on ossification of metacarpal-phalangeal joints (Racey 1974) and female reproductive condition by abdominal palpation and inspection of the mammae. We attached 0.32–0.71-g radiotransmitters (Blackburn Transmitters, Nacogdoches, TX) to the mid-scapular region with Skin Bond® (Smith and Nephew, Inc., Largo, FL) surgical adhesive. Transmitter mass was 1.7–4.7% of bat mass and averaged 3.69% (± 0.21 SE). We tracked each bat to its roost the morning after capture and 5 days/week thereafter from mid-May until August, 2000–2005. We visually located each bat in its roost using binoculars and exit counts. We followed the guidelines of the American Society of Mammalogists for the capture, handling, and care of mammals (Animal Care and Use Committee 1998).

Roost and site data collection

For each roost tree, we recorded tree species and diameter at breast height (dbh), and we measured roost height and total tree height with a clinometer. We characterized forest structure surrounding each roost (site characteristics; Table 1) within a 17.84-m radius (0.10-ha) plot centered on the roost tree. We tallied all woody stems >1 m tall and <5 cm dbh in the 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 cover using a spherical densiometer and averaged those values for each plot.

To identify site characteristics that resulted in a greater likelihood of roosting, we selected a random tree and surrounding 0.10-ha plot for comparison with each roost tree. Because all roosts were in snags, we selected only snags for random trees. We collected identical measurements at random and roost plots. To ensure that random snags were available to bats, we selected random snags by choosing the first snag >5 cm dbh and >40 m distance, at a random azimuth from each roost.

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. We determined forest habitat classes from ONF stand maps of the study area, which we updated and corrected using a 10-m digital color ortho-photoquad (DOQ) from 2001 and ground-truthing (Perry et al. 2007). Pine-woodland restoration and single-tree selection stands were initially treated with similar thinning and mid-story removal; thus, we considered single-tree selection stands and pine-woodland restoration areas a single "thinned mature" class. We defined available habitats based on locations of roosts by creating a 1-km radius circle around each roost location. We then combined all circles and designated the area within this polygon as the available habitat. The 1-km radius circle (314 ha) was smaller than average home range (2906 ha) reported by Menzel et al. (2001) in an urban-forest interface of Georgia, but was close to the average commuting distance between roosts and foraging areas for Big Browns Bats in Ontario (0.9 km; Brigham 1991).

Analyses

We collected data for both males and females. However, sample size for females (n = 9 roosts from 4 individuals) was too low for accurate habitat inferences, model development, or multivariate analysis. Therefore, we did not include data for females in the site analyses, but included information on their roost use. For all analyses, we considered roost the experimental unit, which is the predominant method used in studies of bat roosting (e.g., Elmore et al. 2004, Miles et al. 2006), and assumes that multiple roosts by individuals are independent. We compared characteristics of roost snags (by sex) with random snags using analysis of variance (ANOVA) at alpha = 0.05.

We created a logistic regression model for males that linked forest-stand structural characteristics (site characteristics) with increased likelihood of bat roosting. Because roosts were relatively close to random plots, we used matched-pairs (each roost matched with its corresponding random location) conditional logistic regression (Hosmer and Lemeshow 2000). We used an information-theoretic approach to select the habitat model for males. However, we used an exploratory method to develop candidate models because we lacked sufficient biological information to develop *a priori* models for male Big Brown Bats in the southeastern United States. For our candidate models, we first examined pair-wise correlations and removed variables that correlated ($r \geq 0.70$) with other variables; thus, we included 11 site parameters (Table 1) derived from 0.1-ha plots surrounding roost and random snags. We then used a best-subsets procedure which selected the best 1-variable model, best 2-variable model, and so forth based on values of the chi-square statistic (SAS Institute Inc. 2000). We determined the most parsimonious model among these candidate models based on the value of Akaike's Information Criterion modified for small samples (AIC_c), and we used multi-model inference by averaging parameter estimates of models within 2 units of AIC_{min} (Burnham and Anderson 2002). We used weights (ω_i) calculated among all models within 2 units of AIC_{min} for averaging, and we calculated odds ratios from model-averaged parameter estimates. Odds ratios were the odds of roost/random. We computed weighted unconditional standard errors for each parameter (Burnham and Anderson 2002), and we evaluated the strength of competing models using a generalized R^2 (Nagelkerke 1991).

Results

We located and visually confirmed 25 roosts of 12 adult males and 9 roosts of 4 adult females. Number of roosts per individual was 1–4 for males (mean = 2.1 ± 0.4 SE) and 1–4 for females (mean = 2.3 ± 0.6). All roosts of females were maternity roosts (pups present), and all males roosted alone. All roosts for both sexes were in Shortleaf Pine snags ≥10 cm dbh (range = 13.0–40.5; Fig. 1). Most roost snags (82%) were 15–25 cm dbh. The available density of snags ≥15 cm dbh (from random plots) was 18 hardwood snags/ha and 26 pine snags/ha. One male roost and 1 female colony were in crevices at the top of broken pine snags; all other roosts for both sexes (94%) were under loose exfoliating bark. Female roosts were similar to males; mean height and diameter of snags used for roosting did not differ between sexes, nor did height of roost (Table 2). However, roost snags for both sexes were taller and greater in diameter than random snags. One female roosted alone with 1 pup and remained in the same roost for the duration of her tracking

Table 1. Site characteristics measured in 0.1-ha plots surrounding roost snags of male Big Brown Bats and random snags in the Ouachita Mountains of Arkansas, 2000–2005.

Site parameter	Description
COV[A]	Average overstory canopy cover (%)
Stumps	Number of cut stumps ≥10 cm
Under5	Number of stems <5.0 cm dbh
P5to10	Number of pines 5.0–9.9 cm dbh
H5to10	Number of hardwoods 5.0–9.9 cm dbh
P10to25[B]	Number of pines 10.0–24.9 cm dbh
H10to25[B]	Number of hardwoods10.0–24.9 cm dbh
P≥25	Number pines ≥25.0 cm dbh
H≥25	Number of hardwoods ≥25.0 cm dbh
Psnag≥10	Number of pine snags ≥10 cm dbh
Hsnag≥10	Number of hardwood snags ≥10 cm dbh
Psnag<10	Number of pine snags <10 cm dbh
Hsnag<10	Number of hardwood snags <10 cm dbh

[A]All variables except COV were measured as total number in 0.1-ha plot.
[B]Not included in logistic model for males because of correlation ($r \geq 0.70$) with other parameters.

period (8 days). All other female roosts (89%) were colonies containing ≥2 adults. Based on observations of bats in roosts and exit counts, the number of bats in each female roost (adults and juveniles) was 2–10, and averaged 5.4 (±1.1 SE).

Logistic regression differentiating male roost sites from random sites included 4 models within 2 units of AIC_{min} (Table 3). The parameter-averaged

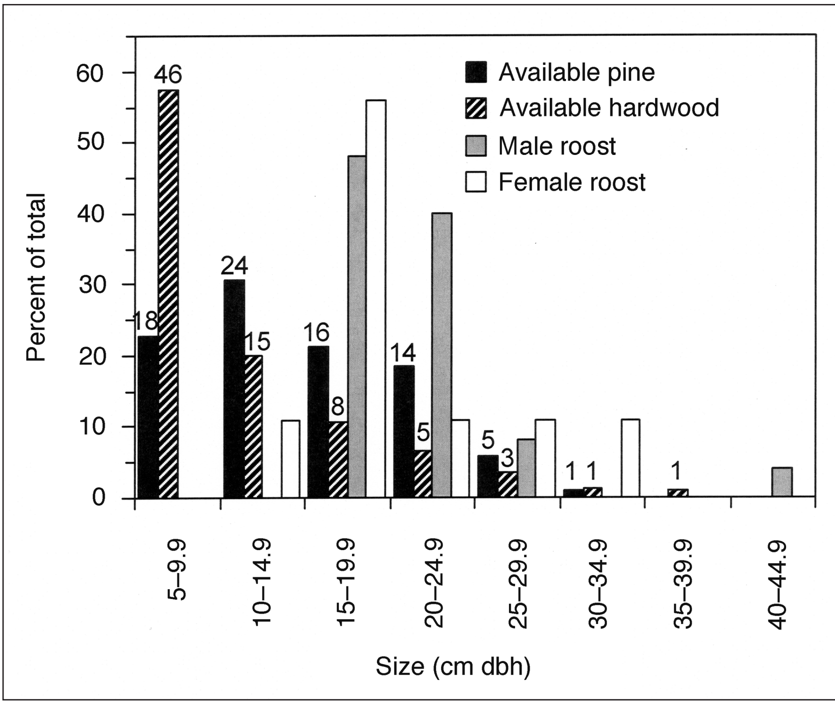

Figure 1. Size distribution (cm dbh) of available pine and hardwood snags (≥5 cm), and proportion of male and female Big Brown Bats roosts in each size class of pine snag in the Ouachita Mountains of Arkansas, 2000–2005. Numbers above columns indicate average available density (snags/ha) of each snag type by size class.

Table 2. Characteristics of roost snags used by male (n = 25) and female (n = 9) Big Brown Bats and comparisons with random snags in the Ouachita Mountains of Arkansas during summer, 2000–2005.

	Female		Male		Random			
Tree characteristic	Mean	SE	Mean	SE	Mean	SE	F	P^A
Snag height (m)	12.3A[B]	1.4	12.0A	0.9	6.5B	0.9	10.2	0.001
Snag diameter (dbh, cm)	20.6A	2.2	21.5A	1.0	15.3B	1.2	7.9	0.001
Roost height (m)	8.3	1.0	7.5	0.5			0.4	0.512

[A]Probability of F based on ANOVA.
[B]Within rows, means with like letter were not significantly different using Tukey-Kramer adjustments to separate means (alpha = 0.05).

model contained the following variables: Stumps (estimate = 0.126 ± 0.073 [unconditional SE]; odds ratio = 1.135), COV (estimate = -0.030 ± 0.028; odds ratio = 0.971), Under5 (estimate = -0.004 ± 0.002; odds ratio = 0.996), P≥25 (estimate = 0.220 ± 0.166; odds ratio = 1.246), Hsnag≥10 (estimate = 0.397 ± 0.238; odds ratio = 1.487), and Psnag<10 (estimate = 0.232 ± 0.225; odds ratio = 1.261). This parameter-averaged model indicated male Big Brown Bats were more likely to roost at sites with open forest conditions derived from recent partial harvesting (less canopy cover and more cut stumps), which contained abundant large overstory pines, hardwood snags ≥10 cm dbh, and small pine snags <10 cm dbh.

Most male roosts (84%) were in partially harvested stands, including thinned mature and group-selection stands (Table 4). Of those roosts, only 1 was in an unharvested greenbelt; thus, 80% of male roost trees were located in recently (<5 years) thinned or partially harvested patches of forest. No roosts were located in hardwood stands (11.4% of available), Loblolly Pine plantations (2.4% of available), or young stands (overstory <50 years old, including Loblolly Pine plantations; 15.7% of available habitat).

Discussion

Snag characteristics

Both sexes of Big Brown Bats roosted in snags that were taller and greater in diameter than random snags; this is a common characteristic of roost

Table 3. Values of AIC_c, difference between AIC_c and AIC_{min} (Δ_i), model weights (ω_i), and generalized R^2 for models within 2 units of AIC_{min} (32.243) that explained differences between roost sites of male Big Brown Bats and random locations in the Ouachita Mountains of Arkansas, 2000–2005. Model parameters are defined in Table 1.

Model[A]	AIC_c	Δ_i	ω_i	R^2
+Stumps[B] +Hsnag≥10	32.721	1.945	0.123	0.24
+Stumps[B] +Hsnag≥10[B] –Under5[B]	30.891	0.115	0.308	0.39
+Stumps +Hsnag≥10 –Under5 +P≥25	30.776	0.000	0.327	0.48
+Stumps[B] +Hsnag≥10[B] –Under5[B] +P≥25[B] –COV +Psnag<10	31.379	0.603	0.242	0.65

[A]+ – = sign of parameter estimate in model.
[B]95% confidence interval for parameter estimate did not contain zero.

Table 4. Percent of roosts (n = 25 roosts) for male Big Brown Bats in 5 forest habitats and percent of each habitat available (derived from merged 1-km radius circles surrounding roosts) in the Ouachita Mountains of Arkansas, 2000–2005.

Forest habitat class	Used	Available
Mixed pine-hardwood group selection	16.0	4.7
Mixed pine-hardwood, thinned mature[A]	68.0	35.9
Unharvested mixed pine-hardwood 50–99 years old	8.0	25.6
Unharvested mixed pine-hardwood ≥100 years old	8.0	5.5
Other habitats	0.0	28.3

[A]Included single-tree selection and pine-woodland restoration areas initially converted from mature (>50 years old) even-aged stands 1–5 years previously.

trees used by most female tree-roosting bats (e.g., Kalcounis-Rüppell et al. 2005, Lacki and Baker 2003). Although hardwood snags (of many species) were abundant throughout the study area and used extensively by other cavity-roosting species including *Myotis septentrionalis* (Trouessart) (Northern Long-eared Bat) and *Nycticeius humeralis* (Rafinesque) (Evening Bat) (Perry and Thill 2007, in press), we found all roosts for both sexes of Big Brown Bats exclusively in Shortleaf Pine snags. In Saskatchewan and northern British Columbia, *Populus tremuloides* Michx. (Aspens) were the primary tree species used for roosting by Big Brown Bats (Kalcounis and Brigham 1998, Parsons et al. 2003, Willis et al. 2006). However, in areas where *P. ponderosa* P. & C. Lawson (Ponderosa Pines) occur, it is one of the primary tree species used for roosting (Betts 1996, Brigham 1991, Cryan et al. 2001, Rabe et al. 1998, Rancourt et al. 2007).

Mature Ponderosa Pine and Shortleaf Pine have similar structural characteristics. They do not have branches on the lower bole and both have thick bark that serves as insulation against fires; these characteristics make both species tolerant to moderate ground-level fires in fire-adapted ecosystems (Burns and Honkala 1990). These characteristics may also make snags of both species favorable roosting sites for bats. For example, Rabe et al. (1998) found most (74%) roosts of 8 species under bark of Ponderosa Pine snags in Arizona, and Perry and Thill's (2007) found 33% of roosts of Northern Long-eared Bats in the Ouachita Mountains were under bark of Shortleaf Pine snags. Bark on dead Shortleaf Pines characteristically exfoliates in sheets >30 cm x 30 cm, which creates relatively large shelters that are closed at the top and open below. Willis et al. (2006) found that cavity use by female Big Brown Bats correlated with available cavity space, with bats roosting more in larger cavities than expected. Similarly, both male and female Big Brown Bats in our study may have selected these pine-bark roosts over other substrates because of the relatively large interior they provided for large-bodied bats.

Unlike cavities in live aspens that were reused by roosting female Big Brown Bats up to 10 years in Saskatchewan (Willis et al. 2003), exfoliating bark is highly ephemeral. For example, the bark covering a maternity colony we located fell off the snag the second day of tracking. We found the bark on the ground at the base of the snag with 6 bats hiding underneath. The following day, the instrumented bat was located in another roost. Thus, bats using such ephemeral roosting structures would require a constant supply of snags of the right age to maintain this seemingly preferred roosting substrate (Hayes 2003).

A December 2000 ice storm with 2–7 cm of accumulation created abundant pine and hardwood snags throughout the study area, and density of Shortleaf Pine snags (≥10 cm dbh) from random plots averaged 26 snags/ha near male roost sites. Consequently, pine snags were abundant and were likely not a limiting factor during the study. Snag densities in forested ecosystems can vary considerably based on a gradient of disturbance and forest successional stage. Density of snags in forests under low levels of disturbance, such as those subjected primarily to lightning strikes, senescence, and occasional disease, are likely lower than areas subjected to frequent intense ground-level burns, widespread insect outbreaks, hurricanes, or ice storms. It is unknown what the roosting habits of Big Brown Bats would be in areas with lower snag densities, and research on optimal densities of snags needed to sustain snag-dependent bats is warranted. Nevertheless, some species such as Big Brown Bats may benefit from these large-scale disturbances.

Forest structure

Although Kalcounis and Brigham (1998) found habitat complexity was not a factor affecting roost selection of female Big Brown Bats in Saskatchewan, we found males selected sites that were less structurally complex than most of the surrounding forests. Roost sites were more likely to have more recently cut stumps (a measure of the number of overstory and mid-story trees removed) and less canopy cover than random plots. Furthermore, most male roosts (68%) were in stands that had been partially harvested, and were in the portions of those stands where the overstory density was reduced and the mid-story was removed. They also rarely roosted in unharvested greenbelts located in partially harvested stands. Similar to our results, Big Brown Bats in South Dakota roosted in relatively open forest stands that were dominated by large trees, had open canopies, and had greater tree spacing than random (Cryan et al. 2001), and Big Brown Bats in Washington selected open forests of Ponderosa Pine and Aspen for roosting over more closed pine habitats (Rancourt et al. 2007). Our model for roost selection indicated male Big Brown Bats in our study area were also more likely to roost at sites with more hardwood snags ≥10 cm dbh and more pine snags 5–10 cm dbh. Although males did not roost in these smaller pine snags or in these larger hardwood snags, large hardwood snags were created as a wildlife management treatment in areas where most male Big Brown Bats roosted (thinned mature stands), and the association between hardwood snags and roosting was likely a result of correlation, not causation. Unlike hardwood snags that were mostly created via management in these areas, small pine snags typically were created naturally, mostly by the ice storm. The greater likelihood of roosts at locations with abundant small pine snags may have resulted from roosts being at sites that were more heavily damaged by the ice storm; density of pine snags 5–10 cm dbh at male roost sites averaged 23.2 snags/ha compared to 19.6 snags/ha at random sites.

Conclusions

Unlike other cavity-roosting bat species that used a variety of tree species in the Ouachita Mountains for roosting (e.g., Perry and Thill 2007), both sexes of Big Brown Bats roosted only in Shortleaf Pine snags despite abundant hardwood snags of many species throughout the study area. Thus, a sustainable supply of shortleaf pine snags would benefit Big Brown Bats in forested landscapes that lack man-made structures. Others studies suggest that large-diameter (>30 cm dbh) snags are necessary for roosting by Big Brown Bats in other areas (e.g., Rabe et al. 1998); however, we found 88% of snags used by males were 15–25 cm dbh, although larger snags may have been limited. Nevertheless, larger snags (>30 cm dbh) do not appear to be vital for roosting by male Big Brown Bats in the Ouachita Mountains.

Because males roosted mostly in relatively open forest conditions when compared to random sites, many silviculture treatments that reduce overall basal area (BA), but maintain a mature (≥50-years-old) overstory, may provide roosting habitat for males. In the Ouachita Mountains, partial-harvest treatments, including single-tree selection or thinning, could initially be attractive sites for roosting if abundant Shortleaf Pine snags are available within those treatments. However, maintaining a sustainable supply of pine snags in areas with reduced overstory BA may be a challenge, and study is needed on the sustainability of pine snags in thinned forests under light to moderate levels of disturbance. Our single-tree selection and group selection areas were in the early stages of transition to uneven-aged stand structure. Whether or not they will provide suitable roosting habitat for Big Brown Bats when they attain an uneven-aged structure (typically 3+ distinct age classes of trees) in future years is unknown. Pine-woodland restoration areas subjected to periodic (3-year interval) controlled burns will likely maintain open forest conditions dominated by large overstory pines, but long-term snag sustainability in those areas is unknown.

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Literature Cited

Agosta, S.J. 2002. Habitat use, diet, and roost selection by the Big Brown Bat (*Eptesicus fuscus*) in North America: A case for conserving an abundant species. Mammal Review 32:179–198.

Animal Care and Use Committee. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. Journal of Mammalogy 79:1416–1431.

Beer, J.R., and A.G. Richards. 1956. Hibernation of the Big Brown Bat. Journal of Mammalogy 37:31–41.

Betts, B.J. 1996. Roosting behavior of Silver-haired Bats (*Lasionycteris noctivagans*) and Big Brown Bats (*Eptesicus fuscus*) in northwest Oregon. Pp. 35–61, *In* R.M.R. Barclay and R.M. Brigham (Eds.). Bats and Forests Symposium, Research Branch, British Columbia Ministry of Forests, 19–21 October 1995, Victoria, BC, Canada. 292 pp.

Brigham, R.M. 1991. Flexibility in foraging and roosting behavior by the Big Brown Bat (*Eptesicus fuscus*). Canadian Journal of Zoology 69:117–121.

Brigham, R.M., and M.B. Fenton. 1986. The influence of roost closure on the roosting and foraging behaviour of *Eptesicus fuscus* (Chiroptera: Vespertilionidae). Canadian Journal of Zoology 64:1128–1133.

Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Second Edition. Springer-Verlag, New York, NY. 488 pp.

Burns, R.M., and B.H. Honkala, (Technical Coordinators). 1990. Silvics of North America: 1 Conifers. US Forest Service, Agriculture Handbook 654. 877 pp.

Cryan, P.M., M.A. Bogan, and G.M. Yanega. 2001. Roosting habits of four bat species in the Black Hills of South Dakota. Acta Chiropterologica 3:43–52.

Elmore, L.W., D.A. Miller, and F.J. Vilella. 2004. Selection of diurnal roosts by Red Bats (*Lasiurus borealis*) in an intensively managed pine forest in Mississippi. Forest Ecology and Management 199:11–20.

Gates, J.E., G.A. Feldhamer, L.A. Griffith, and R.L. Raesly. 1984. Status of cave-dwelling bats in Maryland: Importance of marginal habitats. Wildlife Society Bulletin 12:162–169.

Hamilton, I.M., and R.M.R. Barclay. 1994 Patterns of torpor and day-roost selection by male and female Big Brown Bats (*Eptesicus fuscus*). Canadian Journal of Zoology 72:744–749.

Hayes J.P. 2003. Habitat ecology and conservation of bats in western coniferous forests. Pp. 81–119, *In* C.J. Zabel and R.G. Anthony (Eds.). Mammal Community Dynamics: Management and Conservation in the Coniferous Forests of Western North America. Cambridge University, Cambridge, UK. 550 pp.

Hosmer, D.W., and S. Lemeshow. 2000. Applied Logistic Regression, Second Edition. John Wiley and Sons, Inc. New York, NY. 392 pp.

Kalcounis, M.C., and R.M. Brigham. 1998. Secondary use of aspen cavities by tree-roosting Big Brown Bats. Journal of Wildlife Management 62:603–611.

Kalcounis-Rüppell, M.C., J.M. Psyllakis, and R.M. Brigham. 2005. Tree roost selection by bats: An empirical synthesis using meta-analysis. Wildlife Society Bulletin 33:1123–1132.

Kunz, T.H., and L.F. Lumsden. 2003. Ecology of cavity-and foliage-roosting bats. Pp. 3–89, *In* T.H. Kunz and M.B. Fenton (Eds.). Bat Ecology. The University of Chicago Press, Chicago, IL. 779 pp.

Kurta, A., and R.H. Baker. 1990. *Eptesicus fuscus*. Mammalian Species 356:1–10.

Lacki, M.J., and M.D. Baker. 2003. A prospective power analysis and review of habitat characteristics used in studies of tree-roosting bats. Acta Chiropterologica 5:199–208.

Lacki, M.J., and J.T. Hutchinson. 1999. Communities of bats (Chiroptera) in the Grayson Lake region of Northeastern Kentucky. Journal of the Kentucky Academy of Science 60:9–14.

Lausen, C.L., and R.M.R. Barclay. 2006. Benefits of living in a building: Big Brown Bats (*Eptesicus fuscus*) in rocks versus buildings. Journal of Mammalogy 87: 362–370.

McNab, W.H., and P.E. Avers (Compilers). 1994. Ecological subregions of the United States. USDA Forest Service Administrative Publication WO-WSA-5, Washington, DC.

Menzel, M.A., T.C. Carter, L.R. Jablonowski, B.L. Mitchell, J.M. Menzel, and B.R. Chapman. 2001. Home-range size and habitat use of Big Brown Bats (*Eptesicus fuscus*) in a maternity colony located on a rural-urban interface in the Southeast. Journal of the Elisha Mitchell Scientific Society 117:36–45.

Miles, A.C., S.B. Castleberry, D.A. Miller, and L.M. Conner. 2006. Multi-scale roost selection by Evening Bats on a pine-dominated landscape in southwest Georgia. Journal of Wildlife Management 70:1191–1199.

Mills, R.S., G.W. Barrett, and M.P. Farrell. 1975. Population dynamics of the Big Brown Bat (*Eptesicus fuscus*) in southwestern Ohio. Journal of Mammalogy 56: 591–604.

Mumford, R.E., and J.B. Cope. 1964. Distribution and status of the chiroptera in Indiana. American Midland Naturalist 75:473–489.

Nagelkerke, N.J.D. 1991. A note on a general definition of the coefficient of determination. Biometrika 78:691–692.

Parsons, S., K.J. Lewis, and J.M. Psyllakis. 2003. Relationship between roosting habitats of bats and decay of aspen in sub-boreal forests of British Columbia. Forest Ecology and Management 177:559–570.

Perry, R.W., and R.E. Thill. 2007. Roost selection by male and female Northern Long-eared Bats in a pine-dominated landscape. Forest Ecology and Management 247:220–226.

Perry, R.W., and R.E. Thill. In press. Diurnal roosts of male Evening Bats (*Nycticeius humeralis*) in diversely managed pine-hardwood forests. American Midland Naturalist.

Perry, R.W., R.E. Thill, and D.M. Leslie, Jr. 2007. Selection of roosting habitat by forest bats in a diverse forested landscape. Forest Ecology and Management 238: 156–166.

Rabe, M.J., T.E. Morrell, H. Green, J.C. deVos, Jr., and C.R. Miller. 1998. Characteristics of Ponderosa Pine snag roosts used by reproductive bats in northern Arizona. Journal of Wildlife Management 62:612–621.

Racey, P.A. 1974. Ageing and the assessment of reproduction status of Pipistrelle Bats, *Pipistrellus pipistrellus*. Journal of Zoology 173:264–271.

Rancourt, S.J., M.I. Rule, and M.A. O'Connell. 2007. Maternity roost site selection of Big Brown Bats in Ponderosa Pine forests of the channeled scablands of northeastern Washington State, USA. Forest Ecology and Management 248:183–192.

SAS Institute Inc. 2000. SAS/STAT User's Guide, Version 8 edition. SAS Institute, Cary, NC.

Saugey, D.A., D.R. Heath, and G.A. Heidt. 1989. The bats of the Ouachita Mountains. Proceedings of the Arkansas Academy of Science 43:71–77.

Timpone, J.C., J.G. Boyles, and L.W. Robbins. 2006. Potential for niche overlap in roosting sites between *Nycticeius humeralis* (Evening Bats) and *Eptesicus fuscus* (Big Brown Bats). Northeastern Naturalist 13:597–602.

Tuttle, M.D., and D. Stevenson. 1982. Growth and survival of bats, Pp. 105–150, *In* T.H. Kunz (Ed.). Ecology of Bats. Plenum Press, New York, NY. 425 pp.

Vonhof, M.J. 1996. Roost-site preferences of Big Brown Bats (*Eptesicus fuscus*) and Silver-haired Bats (*Lasionycteris noctivagans*) in the Pend d'Oreille Valley in Southern British Columbia. Pp.62–79, *In* R.M.R. Barclay and R.M. Brigham (Eds.). Bats and forests Symposium, Research Branch, British Columbia Ministry of Forests, 19–21 October 1995, Victoria, BC, Canada. 292 pp.

Whitaker, J.O., Jr. 1995. Food of the Big Brown Bat *Eptesicus fuscus* from maternity colonies in Indiana and Illinois. American Midland Naturalist 134:346–360

Whitaker, J.O., Jr., and S.L. Gummer. 2000. Population structure and dynamics of Big Brown Bats (*Eptesicus fuscus*) hibernating in buildings in Indiana. American Midland Naturalist 143:389–396.

Willis, C.K.R., K.A. Kolar, A.L. Karst, M.C. Kalcounis-Rüppell, and R.M. Brigham. 2003. Medium- and long-term reuse of Trembling Aspen cavities as roosts by Big Brown Bats (*Eptesicus fuscus*). Acta Chiropterologica 5:85–90.

Willis, C.K.R., C.M. Voss, and R.M. Brigham. 2006. Roost selection by forest-living female Big Brown Bats (*Eptesicus fuscus*). Journal of Mammalogy 87:345–350.