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Selection of roosting habitat by forest bats in a diverse forested landscape

Roger W. Perry [a,*], Ronald E. Thill [b], David M. Leslie Jr. [c]

[a] Southern Research Station, USDA Forest Service, P.O. Box 1270, Hot Springs, AR 71902, USA
[b] Southern Research Station, USDA Forest Service, 506 Hayter Street, Nacogdoches, TX 75965, USA
[c] Oklahoma Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, Biological Resources Division,
404 Life Sciences West, Oklahoma State University, Stillwater, OK 74078, USA

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Abstract

Many studies of roost selection by forest-dwelling bats have concentrated on microhabitat surrounding roosts without providing forest stand-level preferences of bats; thus, those studies have provided only part of the information needed by managers. We evaluated diurnal summer roost selection by the bat community at the forest-stand level in a diversely forested landscape in the Ouachita Mountains of central Arkansas. Over a 6-year period, we evaluated 428 roost locations for 162 individual bats of 6 species. Using Euclidean distance analysis and individual bat as the experimental unit, all 6 species were selective ($P < 0.05$) in their choice of roosting habitat. Five of six species preferred ($P < 0.05$) to roost in or near mature ($\geq$50 years old), mixed pine-hardwood forest that had undergone recent partial harvest, midstory removal, and burning; 41.3% of roosts were located in that habitat but it comprised an average of only 22.8% of available habitat. Five of six species also preferred older ($\geq$100 years old), relatively unmanaged, mixed pine-hardwood forest. Although 19.9% of roosts from all species were located in 50- to 99-year-old, second-growth forests of mixed pine-hardwood (average of 21.0% of available habitat), that habitat was preferred by no species of bat. In partially harvested stands, unharvested buffer strips (greenbelts) surrounding ephemeral streams were used at differing levels by each species; most (90%) eastern pipistrelle (*Pipistrellus subflavus*) roosts were in greenbelts whereas few (2.7%) Seminole bat (*Lasiurus seminolus*) roosts were in greenbelts. Older forests, thinned mature forests with reduced midstories, and greenbelts retained in harvested areas were all important roosting habitats for the bat community in the Ouachita Mountains. Our results demonstrate the importance of open forest conditions and a diversity of stand types to bat communities of the southeastern U.S.
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Keywords: Arkansas; Habitat selection; *Eptesicus fuscus*; *Lasiurus*; *Myotis septentrionalis*; *Nycticeius humeralis*; *Pipistrellus subflavus*; Roost selection; Timber harvest

1. Introduction

Because roost sites of bats play an important role in thermoregulation and protection from predators, roost-site characteristics undoubtedly influence bat fitness and survival (Vonhof, 1996). Many tree-roosting bats prefer large-diameter trees and snags for roosting (e.g., Kalcounis, 1995; Vonhof, 1996; Brigham et al., 1997; Crampton and Barclay, 1998), and old-growth forests in the western U.S. and Canada provide abundant large trees and snags that are used by some species (e.g., Crampton and Barclay, 1998; Gellman and Zielinski, 1996). However, in the southeastern U.S., a diverse bat fauna is present (Bat Conservation International, 2001) but little old-growth forest exists and intensive forest management is common throughout much of the region (Conner and Hartsell, 2002; Trani, 2002). Recent research has increased our understanding of roost-tree characteristics in this region, but information on forest-stand preferences for roosting is still insufficient for effective management across most landscapes.

In the Ouachita Mountain region of Oklahoma and Arkansas, bats can be divided into two guilds based on their diurnal roosting habits during summer: those that roost primarily in foliage (leaves or needles) of tree canopies and those that roost in cavities and crevices of live trees and snags. Cavity and crevice-roosting bats roost in cracks, spaces under exfoliating bark, holes in decaying limbs, old woodpecker

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* Corresponding author. Tel.: +1 501 623 1180x108; fax: +1 501 623 0186.
E-mail address: rperry03@fs.fed.us (R.W. Perry).

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holes, and hollow trunks of live trees and snags (Christy and West, 1993). Big brown bats (*Eptesicus fuscus*), evening bats (*Nycticeius humeralis*), and northern long-eared bats (*Myotis septentrionalis*) are cavity- and crevice-roosting species of the Ouachita Mountains. Foliage-roosting bats typically roost by hanging from limbs, leaf petioles, or small branches in tree canopies (Constantine, 1966; Menzel et al., 1998); this guild includes eastern red bats (*Lasiurus borealis*), Seminole bats (*L. seminolus*), and eastern pipistrelles (*Pipistrellus subflavus*).

Many studies of roost selection in forested areas have found roost trees located at sites with lower canopy cover or tree density than random locations (e.g., Kalcounis-Rüppell et al., 2005; Boyles and Aubrey, 2006; Psyllakis and Brigham, 2006), suggesting some bats species may prefer to roost in relatively open forests. Therefore, thinning forests to lower tree density, reducing midstory, burning to reduce woody understory vegetation, and retaining large overstory trees and snags may improve roosting habitat for some bat species. Although these management practices are becoming increasingly more common on public lands in the southeastern U.S. as forest managers strive to restore ecosystems and reduce fuel hazards (e.g., Bukenhofer and Hedrick, 1997; McMahon et al., 1998), more information is needed on effects of these practices on bat roosting.

To determine habitat characteristics that may influence roost selection, many roosting studies compare habitat attributes (e.g., canopy height and tree density) surrounding (typically <20 m) roost sites with attributes of random points. These habitat components are then extrapolated to the stand level. However, forest managers typically apply a finite number of treatments to forest stands that integrate numerous objectives including forest regeneration, economics, fuel reduction, community restoration, and wildlife habitat improvement. Thus, knowing how bats respond to specific silvicultural treatments, stand ages, and forest types is useful information for managers. Furthermore, many studies of bat roosting conducted in forested environments had a limited diversity of forest types and stand ages; true measurements of preference among habitats are limited if a wide array of habitats are not available to the species under study.

To analyze stand-level roost selection by forest bats, past studies used the method of Neu et al. (1974) to compare proportional use of habitats with available proportions, but this method uses locations instead of individuals as the experimental unit, which may bias results (Johnson, 1980; Aebischer et al., 1993; Miller et al., 2003). Furthermore, this analysis is limited in number of habitat classes that can be included because it uses the chi-square goodness-of-fit test which may not be valid when >20% of cells have an expected value of <5 (Conover, 1999). An alternative is Euclidean distance analysis, which uses individuals as the experimental unit, defines habitat availability for each individual separately, and can compare many more habitat classes (Conner and Plowman, 2001). This method compares distances from animal locations to each habitat with distances of random locations to each habitat to determine if animals prefer (are closer to) or avoid (are farther from) habitats. Euclidean distance analysis can also provide insight on animal–habitat associations for both area-based habitat features (habitat types) and linear features such as edges (Conner et al., 2003).

Herein, we used Euclidean distance measurements to evaluate selection of diurnal roosting habitat from late spring to mid summer (summer henceforth) by six species of forest bats in a diverse forested landscape to determine which habitats were preferred or avoided for roosting. Based on published literature, we developed the following predictions regarding how bats respond to different habitats: (1) bats prefer to roost in stands that contain mature, relatively large pines and hardwoods (e.g., Kalcounis, 1995; Vonhof, 1996); (2) bats prefer to roost in relatively open stands with less canopy cover (Kalcounis-Rüppell et al., 2005), lower tree density (Hutchinson and Lacki, 2000; Boyles and Aubrey, 2006; Psyllakis and Brigham, 2006), or little midstory clutter (e.g., Campbell et al., 1996); (3) bats roost in proximity to open areas where they prefer to forage (Mackey and Barclay, 1989; Burford and Lacki, 1995; Grindal and Brigham, 1998; Menzel et al., 2002).

2. Methods

2.1. Study area

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

No residential areas, farms, houses, agricultural lands, or pastures existed within the study portion of the basin. Although most of the basin consisted of mixed shortleaf pine (*Pinus echinata*)-hardwood forests managed by the Ouachita National Forest (ONF) of the U.S. Forest Service (USFS), the basin also contained a mix of other forest types, primarily oak (*Quercus* spp.)-hickory (*Carya* spp.). Twelve percent (778 ha) of the area was intensively managed industrial timberlands (managed by Weyerhaeuser Company) consisting mostly of closed-canopy and older/thinned plantations of loblolly pine (*Pinus taeda*) managed under a 30- to 35-year rotation. Those plantations generally were thinned and pruned at 15–20 years of age. Industrial timberlands contained abundant unharvested buffer strips (streamside management zones; SMZs), approximately 30–100 m wide, established around streams for water-quality protection; those SMZs were typically mature hardwood and mixed pine-hardwood forest.

National forest lands within the basin were divided into six management units (range 513–1791 ha) where different silvicultural treatments were implemented during winter of 1999–2000 (Guldin, 2004). A 1232-ha pine woodland restoration unit was thinned initially and burned with the long-term goal of obtaining an open woodland condition with an abundant herbaceous understory, maintained by periodic (3–5 years) prescribed burns. That area was thinned to 13.8 m^2/ha overstory basal area (BA); 1.1 m^2/ha of the total overstory BA was retained overstory hardwoods. 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 two treatments underwent partial midstory removal whereby most hardwoods <15 cm dbh were felled. A 531-ha small group-selection unit (openings of 0.4–0.81 ha) and a 513-ha large group-selection unit (openings of 2.02–4.05 ha) consisted of patch cuts where about 2.3 m^2/ha of overstory BA (primarily pine) was retained and all other trees were removed or felled. 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. All preceding treatments on national forest lands were subjected to a controlled burn during winter 2001. A 1791-ha unit was managed using a mix of treatments and silvicultural systems, including group selection, single-tree selection, and seed-tree cuts in stands of 16–18 ha. Seed-tree cuts had about 2.3 m^2/ha of retained pine overstory; all other trees were removed or felled.

Ephemeral stream drainages were common throughout the basin. On USFS lands, unharvested 15–50-m wide buffer strips (greenbelts) were established for water-quality protection around each drain. Greenbelts were primarily mixed pine-hardwood forest containing mature (≥50 years old) trees and no cutting or midstory removal was conducted in greenbelts. We estimated greenbelts comprised about 20% of most partially harvested stands (pine woodland restoration areas, single-tree selection, and group selection stands, collectively). In addition, USFS lands also retained SMZs along permanent and intermittent streams; these SMZs were generally wider but similar in forest composition to greenbelts.

The basin also contained an 836-ha, largely untreated block, consisting mostly of mature second-growth pine-hardwood timber. Throughout the basin, stands that were either inoperable (e.g., too steep), in various stages of regeneration, uneconomical to harvest, or dominated by uneconomical forest types such as hardwoods were interspersed within treatments. Thus, with its treatment units, untreated areas, and industrial timberlands, the Winona Basin contained most of the predominant forest types and forest management practices, and many of the successional stages for each forest type that existed in the Ouachita Mountains.

2.2. *Bat capture and radiotelemetry*

From mid-May until late July 2000–2005, we captured bats between 21:00 and 01:30 h CST at 21 trapping areas distributed throughout the basin. We trapped bats for 125 nights using 3–8 mist nets (2.6–12.0 m wide × 2.6 m high). Trapping locations were primarily stream pools but also included forest roads, ponds, bridges, road culverts, and dry creek beds. Bat species, mass, age (juvenile or adult), and sex were recorded using standard procedures (Racey, 1974; Kunz, 1988). We followed guidelines of the American Society of Mammalogists for the capture, handling, and care of mammals (Animal Care and Use Committee, 1998).

We used 0.25–0.71-g radiotransmitters (depending on species of bat) with 11–21-day lifespans to locate bats at their diurnal roost sites from mid-May until early August. Transmitters were bonded to the mid-scapular region with surgical adhesive following partial hair removal. Transmitter load was generally <5% of body mass. We tracked each bat to its roost site the morning following capture and approximately 5 days/week until its signal was lost. After approximate roost location was found with radiotelemetry, we attempted to visually locate bats either from the ground using binoculars or by climbing the tree. We collected global positioning system (GPS) coordinates for each bat using GPS receivers with an estimated accuracy of ±10 m.

2.3. *Vegetation mapping*

We obtained digital maps of forest stand boundaries from the ONF and updated/corrected those data using 10-m digital color orthoquads (DOQ) as templates. We classified USFS stands using the continuous inventory and stand condition management system (CISC) database. Forest type, conditions, and past silvicultural treatments were ground-checked and corrected in the data layer, and tree-core data from most stands were used to verify stand ages. We digitized vegetative class boundaries for industrial timberlands from 10-m DOQs and classified habitats using ground-truthing.

We classified each stand into 1 of 13 forest habitat classes (Table 1). For stands that were primarily even-aged, habitat classifications were based on forest type (pine or hardwood) and age; otherwise, stands were classified based on silvicultural treatment. We differentiated hardwood and pine stands because some species of bat (e.g, Seminole bats) roost primarily in pines, whereas others (e.g., eastern red bats) roost primarily in hardwoods (e.g., Menzel et al., 1998). We delineated stands by age because age in primarily even-aged stands is a major determinant of vertical structure and tree density (both indicators of structural clutter) within forest stands (e.g., Baker et al., 1996). All age classes were based on ages of stands in 2000. Using stand successional stages presented by Baker et al. (1996) for pine types in the southeastern U.S., we derived the following age classes based on field observations of relationships between successional stage and age: stands <15 years old (stand initiation phase); stands 15–29 years old (early stem exclusion phase); stands 30–49 years old (late stem exclusion stage); stands 50–100 years old (understory reinitiation stage); and stands ≥100 years old (old-growth stage). To reduce number of classes included in the analysis, we excluded forest habitat classes that were available to only 1 or 2 species and comprised <1% of available habitat; those habitats included hardwood stands 15–29 and 30–49 years old.

In partially harvested stands on USFS lands, unharvested greenbelts could not be delineated from harvested portions using DOQs. Further, the vast number of those relatively small features made demarcating greenbelt boundaries with GPS unfeasible. Thus, habitat maps did not include greenbelts in partially harvested stands, but we recorded roosts located in greenbelts or in greenbelt edges. We classified larger SMZs

Table 1
Forest habitat classes used to compare habitat selection of six bat species during diurnal summer roosting in the Ouachita Mountains of central Arkansas, 2000–2005

Habitat class	Description
Generally even-aged	
Pine <15 years	Even-aged pines, <15 years old
Pine 15–29 years	Even-aged pines, 15–29 years old
Mixed P/H 30–49 years	Primarily pine with a hardwood component, 30–49 years old
Mixed P/H 50–99 years	Mixed pine and hardwood stands, 50–99 years old; no history of thinning, few controlled burns
Hardwood 50–99 years	Hardwood stands, primarily even-aged, 50–99 year old; no history of thinning, few controlled burns
Older stands	
Mixed P/H $\geq$ 100 years	Mixed pine and hardwood stands, $\geq$100 years old; no history of thinning and $<$1 known controlled burn
Hardwood $\geq$100 years	Hardwood stands $>$100 years old; no history of thinning and $\leq$1 known controlled burn
Partially harvested	
P/H group selection	Mature mixed pine-hardwood stands that had undergone mostly recent ($<$6 years) group selection harvest and matrix thinning
P/H thinned mature	Mature ($>$50 years old) mixed pine-hardwood stands that had undergone recent ($<$6 years) overstory reduction and midstory removal; included single-tree selection stands and pine woodland restoration areas in the early stages of transition to desired future conditions
Pine seed-tree	Seed-tree cuts, open stands with scattered mature pines left for seed production, $<$10 years since harvest
Industrial timberlands	
Closed plantation	Closed-canopy loblolly pine plantations, approximately 14–25 years of age
Thinned plantation	Older/thinned loblolly pine plantations, approximately 20–35 years of age
Clearcut	Young, recently harvested ($<$3 years old) industrial clearcuts

surrounding streams based on their age and timber type, and included these with other stands of like type.

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, we grouped those two treatments into a ‘‘thinned mature’’ class. Industrial timberlands were managed using intensive even-aged management. Most of those lands were loblolly-pine plantations with few overstory hardwoods, which we grouped into three habitat classes: young open clearcuts (approximately $<$10 years of age), closed canopy plantations (approximately 10–18 years of age), and thinned plantations (approximately $\geq$19 years of age). No clearcuts $<$10 years old existed on USFS lands within the study area.

2.4. Analysis

Determining boundaries of ‘‘available’’ habitat is critical in resource selection studies because available habitats must represent areas that are accessible to the animal (Aebischer et al., 1993; Alldredge et al., 1998). Instead of defining habitat availability for all individuals in an arbitrarily delineated study area, we defined habitat availability for each individual separately based on their roost locations. For each individual, we created a 1000-m-radius polygon around each roost location for that individual and then combined all polygons to create the area of available habitat for that individual. We generated 200 random locations within that polygon to compare roost locations with random locations. Limited information is available on home-range sizes of forest bats in the southeastern U.S. Although the 1000-m radius is less than the average distance between roost and foraging areas reported for big brown bats in Canada (1800 m; Brigham, 1991), it corresponded roughly with average maximum distance traveled by red bats during foraging in forested environments of the southeastern U.S. (Elmore et al., 2005), and average distance (1137 m) between roost locations and foraging areas for eastern pipistrelles in Georgia (Krishon et al., 1997). Thus, selection estimates were at a scale similar to Johnson’s (1980) third-order selection (selection of sites within an animal’s home range).

We used Euclidean distance statistics (Conner and Plowman, 2001; Conner et al., 2003) to compare roost and random locations. We determined distance to nearest representative of each habitat class from each random and roost location, and created a ratio of use for each forest habitat class by dividing mean roost distance by mean random location distance; we standardized ratios by subtracting 1. Because individual bats frequently roosted in different roosts within the same general area over multiple days, roost locations for individuals were not independent (Hurlbert, 1984). To eliminate this spatial autocorrelation, we considered individual bats as experimental units by averaging distances to each habitat for each individual. We used a separate MANOVA (PROC GLM; SAS Institute Inc., 2000) as the global significance test for each species of bat to determine if the vector of standardized ratios differed from a vector of 0s. For each species, if MANOVA results indicated that an overall difference existed in proximity to the 13 habitat types between roost and random locations, we used t-tests to determine if individual habitats were preferred or avoided. If the ratio was $<$0, roosts were located closer to that habitat than random (preferred); if the ratio was $>$0, the habitat was avoided. We had sufficient numbers of individuals of each sex to compare habitat selection by gender for only eastern red bats and northern long-eared bats. For those two species, we conducted analyses by gender and for combined sexes. We used positive false discovery rate (pFDR) q-values (Storey, 2002) to limit the proportion of Type I errors among post hoc univariate tests. We evaluated all tests at $\alpha = 0.05$.

Table 2
Numbers of individual bats (by sex) and numbers of diurnal summer roosts for six species of bat included in analyses of roost selection in the Ouachita Mountains of central Arkansas, 2000–2005

Species	No. of individuals		No. of roosts per individual		Total no. of roosts
	Male	Female	Range	Mean	
Big brown bat	12	4	1–5	2.1	34
Northern long-eared bat	21	21	1–7	2.4	102
Evening bat	17	0	1–8	2.5	45
Eastern red bat	22	20	1–9	3.5	145
Seminole bat	17	0	1–6	3.0	51
Eastern pipistrelle	21	7	1–5	1.8	49
Total	110	52	1–9	2.8	426

Because results of Euclidean distance statistics may require substantial interpretation (Dussault et al., 2005; Conner et al., 2005), we calculated percent of available habitat and percent of roosts in each habitat class to aid in interpretation. To determine habitat availability for each species, we combined all 1000-m polygons surrounding roost locations for that species into a single polygon and calculated percent of each forest habitat class within this combined polygon. During the 6 years of study, industrial timberlands in the basin underwent harvest and thinning, which changed yearly proportions of young clearcuts, closed-canopy pine plantations, and thinned pine plantations. Therefore, we used a weighted average to represent proportional availability of those habitats during the entire study period.

3. Results

Over 6 summers, we captured 715 bats during 344 net nights. We located 426 roosts from 162 individuals of 6 species: big brown bats, evening bats, northern long-eared bats, eastern red bats, Seminole bats, and eastern pipistrelles (Table 2). We captured no adult female Seminole or evening bats in the basin from late spring to mid summer. For the 2 species with sample sizes large enough to analyze by sex, we obtained 72 male and 73 female roosts for eastern red bats and 55 male and 47 female roosts for northern long-eared bats. Overall MANOVA results indicated selection occurred among the 13 forest habitat classes for each of 6 bat species.

3.1. Cavity- and crevice-roosting species

3.1.1. Big brown bats

Distances to 13 forested habitat classes differed between roost and random locations for combined genders of big brown bats (Wilk's $\lambda = 0.008$; $F = 26.97$; d.f. = 13, 3; $P = 0.010$). Big brown bats preferred to roost in or near thinned mature (recently treated pine woodland restoration areas and single-tree selection stands collectively) and mixed pine-hardwood ≥100 years old (Table 3); no habitats were avoided. Most (52.9%) roosts of big brown bats were in thinned mature habitat, followed by group selection (26.5%; Table 4). In those two habitats, 11% of roosts in thinned mature stands were located in unharvested greenbelts or greenbelt edges, and 22% of roosts in group selection were in greenbelts. All roosts of big brown bats were in pine snags.

Table 3
Mean standardized Euclidean distance ratios for roosting habitat selection among 13 forest habitat classes and t-test probability values comparing distance ratios to each habitat with a value of 0 for 6 species of bats in the Ouachita Mountains of central Arkansas, 2000–2005

Habitat class	Big brown ($n = 16$)[a,c]		Evening ($n = 17$)[b,c]		N. long-eared ($n = 42$)[a,c]		Red ($n = 42$)[a,c]		Seminole ($n = 17$)[b,c]		E. pipistrelle ($n = 28$)[a,c]	
	Mean	$P > \|t\|$	Mean	$P > \|t\|$	Mean	$P > \|t\|$	Mean	$P > \|t\|$	Mean	$P > \|t\|$	Mean	$P > \|t\|$
National forest lands												
Pine <15 years	−0.005[d]	0.913	0.019	0.736	−0.010	0.790	−0.009	0.796	0.064	0.273	0.040	0.437
Pine 15–29 years	−0.134	0.147	−0.081	0.328	−0.004	0.915	0.003	0.961	0.142	0.011*	0.068	0.240
Mixed P/H 30–49 years	−0.001	0.983	0.049	0.313	−0.060	0.177	0.060	0.072	−0.114	0.124	0.029	0.408
Mixed P/H 50–99 years	−0.123	0.452	−0.049	0.780	−0.110	0.215	−0.067	0.429	0.139	0.012*	−0.182	0.045
Mixed P/H ≥ 100	−0.256	0.007*	−0.165	0.021*	−0.193	0.000*	−0.055	0.249	−0.195	0.021*	−0.311	0.000*
Hardwood 50–99 years	0.088	0.360	0.035	0.892	−0.107	0.159	−0.090	0.316	0.139	0.012*	−0.357	0.000*
Hardwood ≥100 years	−0.042	0.127	−0.005	0.788	−0.032	0.000*	−0.086	0.020*	−0.035	0.175	0.013	0.485
P/H group selection	−0.184	0.091	−0.089	0.265	−0.151	0.056	−0.252	0.000*	−0.232	0.050	−0.227	0.012*
P/H thinned mature	−0.584	0.000*	−0.657	0.000*	−0.506	0.000*	−0.307	0.000*	−0.599	0.000*	−0.175	0.149
Pine seed-tree	−0.078	0.057	−0.079	0.072	−0.089	0.000*	0.001	0.910	−0.032	0.574	−0.024	0.000*
Industrial timberlands												
Closed plantation	−0.017	0.729	−0.105	0.091	−0.068	0.037	−0.068	0.048	0.011	0.569	−0.173	0.000*
Thinned plantation	−0.018	0.449	−0.103	0.240	−0.011	0.697	−0.043	0.266	−0.055	0.543	−0.134	0.065
Clearcut	0.003	0.821	−0.011	0.334	−0.010	0.349	0.009	0.349	−0.011	0.610	−0.034	0.151

[a] Both sexes combined.

[b] Males only.

[c] Number of individuals included in the analysis.

[d] Distance ratios = (mean distance from roost location to habitat/mean distance from random location to habitat) −1; values <0 (negative) indicate roosts were closer to a habitat than random, values >0 (positive) indicate roosts were further from a habitat than random.

* Significant at $\alpha = 0.05$ using pFDR q-value (Storey, 2002).

Table 4
Available habitat (%) in 13 forest habitat classes and percent of roosts in each class for 6 species of forest bats in the Ouachita Mountains of central Arkansas, 2000–2005

Habitat	Big brown (n = 34)[a,c]		Evening (n = 47)[b,c]		N. long-eared (n = 102)[a,c]		Red (n = 145)[a,c]		Seminole (n = 51)[b,c]		E. pipistrelle (n = 49)[a,c]	
	Available	Roost	Available	Roost	Available	Roost	Available	Roost	Available	Roost	Available	Roost
National forest lands												
Pine <15 years	2.8	0	2.8	0	3.3	0	3.1	0	3.5	0	3.3	0
Pine 15–29 years	5.3	0	5.1	0	4.9	0	7.6	2.1	8.6	0	7.6	0
Mixed P/H 30–49 years	3.5	0	3.4	0	4.9	1.0	4.4	0	5.0	2.0	3.7	0
Mixed P/H 50–99 years	21.8	14.7	21.3	19.1	22.3	22.5	23.5	24.8	20.6	2.0	16.2	22.4
Mixed P/H > 100	4.5	5.9	4.4	0	4.9	2.9	2.7	2.8	5.2	11.8	8.6	8.2
Hardwood 50–99 years	12.3	0	12.1	17.0	14.0	3.9	12.2	15.2	4.3	0	10.1	34.7
Hardwood >100 years	0	0	2.3	0	1.6	1.0	3.0	8.3	3.0	0	0.2	0
P/H Group selection	17.4	26.5	17.0	6.4	17.5	17.6	12.9	13.8	10.4	11.8	16.0	14.3
P/H thinned mature	28.8	52.9	28.1	57.4	18.4	49.0	16.1	28.3	23.4	60.8	21.9	20.4
Pine seed-tree	0.9	0	0.9	0	1.1	0	1.0	0	0.8	0	1.0	0
Industrial timberlands												
Closed plantation	1.9	0	2.4	0	5.3	1.0	6.2	1.4	1.4	0	6.2	0
Thinned plantation	0.8	0	0.2	0	1.5	1.0	6.8	3.4	13.2	11.8	3.8	0
Clearcut	0.0	0	0.0	0	0.3	0	0.5	0	0.6	0	1.4	0

[a] Both sexes combined.
[b] Males only.
[c] Number of roosts included in the analysis.

3.1.2. *Evening bats*

Distances to 13 forested habitat classes differed between roost and random locations for male evening bats (Wilk's $\lambda = 0.043$; $F = 6.87$; d.f. = 13, 4; $P = 0.038$). Roosts of male evening bats were closer than random locations to thinned mature and mixed pine-hardwood $\geq$100 years old; no habitats were avoided (Table 3). Most (57.4%) roosts were located in thinned mature forest. Although 36.1% of roosts were in 50- to 99-year-old stands of mixed pine-hardwood or hardwood that had not been harvested or thinned (Table 4), those two habitats were not preferred (Table 3). In thinned mature stands, 48.1% of roosts were located in unharvested greenbelts or greenbelt edges, and 66.7% of roosts in group selection were located in those areas. Most (60%) roosts of evening bats were in snags.

3.1.3. *Northern long-eared bats*

Distances to 13 forested habitat classes differed between roost and random locations for combined sexes of northern long-eared bats (Wilk's $\lambda = 0.178$; $F = 10.31$; d.f. = 13, 29; $P < 0.001$). Northern long-eared bats preferred to roost in association with thinned mature, pine seed-tree stands, and hardwood/mixed pine-hardwood $\geq$100 years old; no forest habitat class was avoided (Table 3). Most (49.0%) roosts were located in thinned mature habitats, followed by mixed pine-hardwood 50–99 years old (22.5%), and group-selection (17.6%; Table 4). Most (88%) northern long-eared bat roosts were in snags.

When analyzed by gender, distances to 13 forested habitat classes differed between roost and random locations for female northern long-eared bats (Wilk's $\lambda = 0.073$; $F = 7.78$; d.f. = 13, 8; $P = 0.003$). Females roosted closer to thinned mature ($P < 0.001$), pine-hardwood $\geq$100 years old ($P = 0.001$), hardwood $\geq$100 years old ($P = 0.002$), group-selection ($P = 0.017$), and seed-tree cuts ($P = 0.022$) than random. No habitats were significantly avoided by females. For females, roosts were located in the following habitats: thinned mature (57.4%), mixed pine-hardwood 50–99 years old (21.4%), group selection (17.0%), hardwood 50–99 years old (2.1%), and pine 30–49 years old (2.1%). For the two partially harvested habitat classes, 22.2% of roosts in thinned mature were located in greenbelts or greenbelt edges, and 37.5% of roosts in group-selection were located in those unharvested buffers.

Distances to 13 forested habitat classes differed between roost and random locations for male northern long-eared bats also (Wilk's $\lambda = 0.113$; $F = 4.85$; d.f. = 13, 8; $P < 0.016$). Males roosted closer to thinned mature ($P < 0.001$), pine-hardwood $\geq$100 years old ($P = 0.014$), and seed-tree stands ($P = 0.016$) than random; no forest habitat class was significantly avoided by males. For males, roosts were located in the following habitats: thinned mature (41.8%), mixed pine-hardwood 50–99 years old (23.6%), group selection (18.2%), hardwood 50–99 years old (5.5%), mixed pine-hardwood $\geq$100 years old (5.5%), hardwood $\geq$100 years old (1.8%), closed canopy loblolly plantations (1.8%), and thinned loblolly plantations (1.8%). For the two partially harvested habitats, 47.8% of roosts in thinned mature stands were located in greenbelts or greenbelt edges, and 30.0% of roosts in group-selection were located in greenbelts.

3.2. *Foliage-roosting species*

3.2.1. *Eastern red bats*

Distances to 13 forested habitat classes differed between roost and random locations for combined genders of red bats (Wilk's $\lambda = 0.13$; $F = 14.92$; d.f. = 13, 29; $P < 0.001$). Red bat roosts for both sexes combined were closer than random locations to thinned mature, group selection, and hardwood ≥100 years old; no habitat classes were avoided (Table 3). For both sexes combined, most (28.3%) roosts were in thinned mature habitats, followed by mixed pine-hardwood 50–99 years old (24.8%), and hardwood 50–99 years old (15.2%; Table 4).

When analyzed by gender, distances to 13 forest habitat classes differed between roost and random locations for female red bats (Wilk's $\lambda = 0.058$; $F = 8.69$; d.f. = 13, 7; $P = 0.004$). Females roosted significantly closer to thinned mature ($P < 0.001$) than random; no habitats were significantly avoided by female red bats. Female roosts were located in the following habitats: mixed pine-hardwood 50–99 years old (28.8%), thinned mature (21.9%), group selection (17.8%), hardwood ≥100 years old (12.3%), hardwood 50–99 years old (11.0%), thinned loblolly pine plantations (6.8%), and closed-canopy loblolly plantation (1.4%). For the two partially harvested habitats, 62.5% of female roosts in thinned mature stands were located in greenbelts or greenbelt edges, and 53.8% of roosts in group-selection stands were located in those unharvested buffers.

Distances to 13 forested habitat classes differed between roost and random locations for male red bats as well (Wilk's $\lambda = 0.086$; $F = 7.34$; d.f. = 13, 9; $P = 0.003$). Male red bats roosted closer to group-selection ($P = 0.007$) than random. Male red bat roosts were located in the following habitats: thinned mature (34.7%), mixed pine-hardwood 50–99 years old (20.8%), hardwood 50–99 years old (19.4%), group selection (9.7%), mixed pine-hardwood ≥100 years old (5.6%), hardwood ≥100 years old (4.2%), pine 15–29 years old (4.2%), and closed-canopy loblolly plantation (1.4%). For the two partially harvested habitats, 36.0% of male roosts in thinned mature stands were located in greenbelts or greenbelt edges, and 57.1% of roosts in group-selection stands were located in those unharvested buffers.

3.2.2. *Seminole bats*

Distances to 13 forested habitat classes differed between roost and random locations for male Seminole bats (Wilk's $\lambda = 0.004$; $F = 69.26$; d.f. = 13, 4; $P < 0.001$). Roosts of male Seminole bats were closer than random to thinned mature and mixed pine-hardwood ≥100 years old (Table 3). That species avoided 50–99 year old stands of hardwood or mixed pine-hardwood, and pine 15–29 years old. Most (60.8%) roosts of Seminole bats were in thinned mature habitats (Table 4). Only 14.8% of Seminole bat roosts were located in stands that were not partially harvested or thinned. For the two partially harvested habitat classes, only one roost was located in a greenbelt, all other roosts in those stands were located in harvested portions of stands.

3.2.3. *Eastern pipistrelles*

Distances to 13 forested habitat classes differed between roost and random locations for combined sexes of eastern pipistrelles (Wilk's $\lambda = 0.35$; $F = 31.49$; d.f. = 13, 15; $P < 0.001$). Eastern pipistrelles roosted closer than random to group selection, mixed pine-hardwood ≥100 years old, hardwood 50–99 years old, pine seed-trees, and closed-canopy loblolly pine plantations; no forest habitat class was significantly avoided (Table 3). Most (57.1%) pipistrelle roosts were in hardwood or mixed pine-hardwood stands 50–99 years old. Although 34.7% of roosts were located in partially harvested stands (Table 4), 90.0% of roosts in thinned mature and 85.7% of roosts in group selection were in greenbelts or greenbelt edges.

3.3. *All bat species*

Based on availability to all bat species, the most abundant habitat class was thinned mature (average of 22.8% of available habitat among all species), followed by unharvested mixed pine-hardwood 50–99 years old (21.0%), and group selection (15.2%; Table 4). The habitat containing most roosts was thinned mature (41.3% of roosts were located in this habitat class), followed by mixed pine-hardwood forest 50–99 years old (19.9% of roosts), and group selection (14.7% of roosts). No roosts were located in pine seed-trees or recent clearcuts. Based on analyses of Euclidean distances, the two most preferred habitats were thinned mature and mixed pine-hardwood ≥100 years old; five of six species roosted significantly closer to those habitats than random (Table 3). However, mixed pine-hardwood ≥100 years old comprised an average of only 5.1% of available habitat. Mixed pine-hardwood 50–99 years old was the second most abundant habitat class available, and the second most used habitat (19.9% of roosts), but distance statistics indicated it was not preferred by any species. Recently harvested group selection stands were the third most used stands (14.7% of roosts) and two bat species preferred that habitat class based on distance statistics; probabilities were slightly above alpha ($P = 0.05$–0.10) for big brown, Seminole, and northern long-eared bats.

4. Discussion

Consistent with predictions 1 and 2, bats generally preferred roosting in areas with relatively low tree density and abundant large overstory trees. Five of six species preferred to roost in close proximity to thinned mature habitats, and 41.3% of all roosts were located in that habitat class. That habitat class consisted of mixed pine-hardwood forest that had undergone recent partial harvesting and midstory removal (single-tree selection and pine woodland restoration areas). Those stands were relatively open, had little or no midstory, and contained approximately 13.8 m^2/ha BA of larger overstory pines and hardwoods. These findings are consistent with other studies that found bats prefer to roost at sites with relatively lower tree density (e.g., Hutchinson and Lacki, 2000; Boyles and Aubrey, 2006; Psyllakis and Brigham, 2006), lower canopy coverage (e.g., Kalcounis-Rüppell et al., 2005), and little understory vegetation (e.g., Campbell et al., 1996; Boyles and Aubrey, 2006). For example, Campbell et al. (1996) found that roost sites had less canopy closure, lower understory density, and lower understory height compared with random areas, and Boyles and Aubrey (2006) found all evening bat roosts in stands that were subjected to controlled burning; these stands had greater canopy light penetration than unburned stands. Prior to European settlement of North America, oak and pine woodlands maintained by periodic fire were once abundant throughout the southeastern U.S. (including the Ozark and Ouachita Mountain physiographic region); these ecosystems had open overstories, relatively low BA, and primarily herbaceous understories (Masters et al., 1995; Lorimer, 2001). Open forest conditions of thinned mature stands in our study may have approximated those historical forest conditions.

Possible reasons why bats may prefer to roost in relatively open forest stands include ease of navigation due to reduced clutter, predator avoidance, facilitation of roost relocation, and thermal regulation (Vonhof, 1996). Studies suggest reduced structural clutter facilitates navigation and many species are known to forage in relatively open habitats (Mackey and Barclay, 1989; Burford and Lacki, 1995; Menzel et al., 2002, 2005). Thus, bats may have roosted in or near these relatively open stands to reduce travel time between roosting and foraging habitat. Reduced clutter around roosts also could facilitate detection of predators (Vonhof, 1996). Furthermore, open forest conditions allow more direct sunlight on tree trunks and canopies, which may have thermal benefits for developing young (Racey and Swift, 1981; Vonhof, 1996).

Favorable roosting conditions in some stands that were created immediately after partial harvesting and midstory removal are likely ephemeral. The majority of partial harvesting in the basin was conducted in winter 1999–2000. For single-tree and group-selection stands, that harvest was the first of many entries into those stands. The goal of single-tree selection management is to maintain ≥ 3 distinct age classes of trees within a stand (Baker et al., 1996). Group-selection management involves creating new group openings approximately every 10 years (in this region), which leads to spatial heterogeneity throughout the stand. Over time, the single-tree and group-selection stands will likely increase in clutter and tree density as additional cohorts of trees regenerate. However, little information is available on the long-term effects of uneven-aged management on roost selection by forest bats. In contrast, pine woodland restoration areas, if burned frequently enough to maintain an open, park-like conditions, should provide sustained open forests for roosting if important substrates such as overstory hardwoods and snags remain available.

Our results suggest that spatially heterogeneous stands may be important to the roosting ecology of some species. Most partially harvested stands on USFS lands (pine woodland restoration areas, single-tree selection, and group-selection stands) contained abundant greenbelts, and those greenbelts (along with openings in group selection stands) created heterogeneous conditions within those stands. In partially harvested stands, 88.0% of eastern pipistrelle roosts, 50.0% of male evening bat roosts, and 49.2% of eastern red bat roosts were in greenbelts or greenbelt edges. Alternatively, only 33.8% of northern long-eared bat, 14.8% of big brown bat, and 2.7% of Seminole bat roosts in those stands were in greenbelts. Thus, some species such as pipistrelles relied heavily on greenbelts in partially harvested stands and other species such as Seminole bats rarely used them for roosting. Because greenbelts were primarily around ephemeral drains that did not hold water except during heavy rain events, use of those areas likely was attributed to their structure and placement in the landscape rather than the presence of water. Greenbelts were primarily unharvested pine/hardwood 50–99 years old, and stands of that habitat class were abundant throughout the basin (an average of 21.0% of available habitat) but were not preferred by any species. Thus, adjacency to open habitats and abundant roosting substrate may have made greenbelts attractive roost sites for eastern pipistrelles, and to a lesser extent, red bats and male evening bats. If greenbelts had not been present, extent of roosting by those three species in partially harvested stands is unclear.

Although mature, generally even-aged, mixed pine-hardwood forest 50–99 years of age was the second most abundant habitat available to bats (21.0%) and the second most utilized habitat (19.9% of roosts), distance statistics indicated no species of bat preferred that habitat. Hardwood forests in that age class were preferred only by eastern pipistrelles. Both of those habitat classes were avoided by Seminole bats. Both mixed pine-hardwood and hardwood stands 50–99 years old consisted of second-growth forests that received limited management and were moderately cluttered with midstory trees. These relatively unmanaged second-growth forests likely do not represent optimal roosting habitat for species such as Seminole bats. Older (≥ 100 years old) pine-hardwood stands, although not abundant in the basin (average of only 5.1% of available habitat), were preferred by the three cavity- and crevice-roosting species, eastern pipistrelles, and Seminole bats; older hardwood stands were preferred by northern long-eared bats and red bats. Those results were consistent with studies that found many bats species prefer older forest stands (e.g., Crampton and Barclay, 1998).

The three cavity- and crevice-roosting species relied on snags (to varying degrees) for roosting. Abundance of these species may be limited by snag availability (Brigham et al., 1997), and without snag creation (via management or natural disturbance) some preferred habitats may lack adequate densities of snags. Different forest habitat classes may differ in abundance of large snags. For example, snag densities in South Carolina were highest in hardwood forest types and lowest in pine plantations; intermediate age classes had higher snag densities than older or younger stands of the same type (Moorman et al., 1999). An ice storm in during winter 2000–2001 created abundant pine, and to a lesser extent, hardwood snags throughout the basin. Hardwood snag creation also was included in the harvest prescriptions for single-tree selection and pine woodland restoration areas. Thus, it was unlikely that most habitat classes lacked abundant snags. Relatively open portions of partially harvested stands contained localized areas with large concentrations of pine snags that resulted from ice damage. Many roosts (especially maternity colonies of northern long-eared bats) were located in those snag concentrations. Owen et al. (2002) suggested northern long-eared bats selected localized areas of abundant snags for roosting that provided multiple alternative roost sites. Nevertheless, long-term snag population dynamics under different silvicultural systems and stand densities in the southeastern U.S. are largely unknown and warrant further research.

There appeared to be partitioning in roosting habitat among foliage-roosting species. Male Seminole bats were associated primarily with open stands that retained scattered, relatively large (generally >22.0 cm dbh) overstory pines, and that species rarely roosted in hardwood stands, relatively dense stands, or in unharvested greenbelts. In addition, 12% of Seminole roosts were in thinned pine plantations on industrial timberlands. Our results suggest that Seminole bats (at least males) may have been associated with the vast pine woodlands that were historically abundant across the southeastern U.S. (Lorimer, 2001). In contrast, eastern pipistrelles tended to roost in stands that were more structurally complex, with higher overstory tree densities and abundant midstory hardwoods. In group-selection and thinned mature stands, their roosts were usually in unharvested greenbelts that were more structurally cluttered than the surrounding treated stand, and greenbelts are likely an important habitat component for this species in areas that have undergone harvesting. In our study, red bats (which roosted primarily in foliage of hardwoods) roosted mostly in thinned and unharvested stands (>50 years old) that contained mature overstory hardwoods. In partially harvested stands, they frequently roosted in both greenbelts and harvested portions of stands. Red bats are likely flexible in their habitat selection, and select habitats based on presence of overstory hardwoods. However, they will occasionally roost in pines in industrial forest landscapes (Elmore et al., 2004).

Euclidean-distance analysis suggested eastern pipistrelles and northern long-eared bats preferred seed-tree cuts, but no roosts were located in that habitat class. Distance ratios also indicated that eastern pipistrelles roosted closer to closed-canopy loblolly pine plantations than random, but no pipistrelles roosted in that habitat. Seed-tree cuts were open habitats that were located in areas of the basin where little other recent harvesting was conducted. Openings in areas of continuous forest are frequently used for foraging by bats and many species may prefer to forage in those areas (Burford and Lacki, 1995; Grindal and Brigham, 1998; Menzel et al., 2002; Owen et al., 2004), and bats may have selected roost sites close to these open areas. However, closed-canopy, loblolly pine plantations stands were likely the least usable habitats for roosting in the basin. They were virtually impenetrable to bats; they were dense and cluttered, with high BAs, few hardwoods, and no large snags. The association between pipistrelles and this habitat class may have been an edge effect. Many bat species tend to forage and commute in edge habitats (Ekman and deJong, 1996; Grindal and Brigham, 1999; Verboom and Spoelstra, 1999; Hogberg et al., 2002), and boundaries between those plantations and adjacent stands provided the hardest edges in the study area. Nevertheless, reasons why Euclidean distance analysis indicated these habitats influenced roost selection positively are somewhat equivocal, and may be a result of potential problems associated with Euclidean distance analysis (Dussault et al., 2005).

Our results demonstrate the importance of relatively open forest stands to many bat species in the Ouachita Mountains. Five of six species preferred to roost in proximity to forested habitats that were relatively open and contained mature (>50 years old) overstory trees; these stands resulted from recent partial harvesting, midstory removal, and controlled burning. Although forest stand density had a substantial effect on roost selection, forest type was also important. Species that roosted almost exclusively in pines (seminole bat and big brown bat) roosted more in pine-dominated habitats whereas species that roosted almost exclusively in hardwoods (red bat and eastern pipistrelle) roosted mostly in habitats that contained abundant deciduous hardwoods. Our results indicate that a variety of forest stand conditions, both pine and hardwood, that retain moderate densities (e.g., 13 m^2/ha BA) of mature (>50 years old) overstory trees should be maintained to insure adequate roosting habitat is available for the bat community. Relatively unmanaged older forests (>100 years old), thinned mature (>50 years old) forests with reduced midstories, and greenbelts retained in harvested areas were all important roosting habitats for the bat community in the Ouachita Mountains.

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