Summer Roost Tree Selection by Eastern Red, Seminole, and Evening Bats in the Upper Coast Plain of South Carolina

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Abstract: We radiotracked 6 eastern red *(Lasiurus borealis),* 6 Seminole *(Lasiurus seminolus),* and 24 evening bats *(Nycticeius humeralis)* to 55, 65, and 61 day-roosts, respectively, during summers 1996 and 1997 in the Upper Coastal Plain of South Carolina. For each species, we tested for differences between used roost trees and randomly located trees. We also tested for differences between habitat characteristics surrounding roost trees and randomly located trees. Eastern red and Seminole bats generally roosted in canopies of hardwood and pine *(Pinus),* respectively, clinging to foliage and small branches. Evening bats roosted in cavities or under exfoliating bark in pines and dead snags. Bats selected roost trees with larger dbh and greater height than randomly located trees. Habitat surrounding red bat roosts tended to have greater overstory height, greater basal area, greater woody understory diversity and evenness, greater overstory richness, diversity, and evenness, higher overstory canopy cover, and lower percent pine than randomly located plots. Habitat surrounding Seminole bat roosts had greater basal area, lower woody understory richness, and less Spanish moss *(Tillandsia usneoides)* than randomly located plots. Habit surrounding evening bat roosts had fewer understory and overstory stems, greater overstory height, less overstory richness, lower overstory canopy cover, and more snags than randomly located plots. Forest management strategies that promote longer rotations, complex canopy structure, and snag formation should be beneficial for providing eastern red, Seminole, and evening bats with roosts in the Upper Coastal Plain.

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Many environmental factors such as environmental contaminants (Clark 1988), destruction of foraging habitat (Hill and Smith 1984), and hibernacula disturbance (Tuttle 1979) have been postulated as contributors to declining bat populations. Roost destruction may be the most important factor negatively impacting tree-roosting bats (Kunz 1982, Vonhof and Barclay 1996). An understanding of roost requirements of tree-roosting bats in intensively managed forests is critical for successful conservation and management of these taxa.

There is a paucity of quantitative data on roosts of eastern red, Seminole, and evening bats in the Southeast and most information is limited to anecdotal accounts. Eastern red bat roosts have been observed in Spanish moss (Jennings 1958, Constantine 1966) and hardwood foliage (Barbour and Davis 1969, Koontz and Davis 1991, Menzel et al. 1998). Seminole bat roosts have been observed in Spanish moss (Harper 1927, Constantine 1966, Barbour and Davis 1969, Wilkins 1987), hardwood and pine foliage (Sealander and Heidt 1990, Menzel et al. 1998), and under exfoliating bark (Sealander 1979). Evening bat roosts have been located in Spanish moss (Jennings 1958), buildings (Hooper 1939, Anderson 1951, Cope et al. 1961, Baker and Ward 1967, Easterla and Watkins 1970, Chapman and Chapman 1990), tree cavities (Barbour and Davis 1969, Menzel et al. 1999) and under exfoliating bark (Barbour and Davis 1969, Menzel et al. 1999). We investigated roost-tree characteristics and surrounding site characteristics of roost trees used by eastern red, Seminole, and evening bats in a managed forest landscape in the Upper Coast Plain of South Carolina.

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Methods

This study was conducted on the Savannah River Site (SRS) in the Upper Coastal Plain of west-central South Carolina located about 25 km southeast of Augusta, Georgia. Approximately 90% of the 79,900-ha site is forested. Major forest habitats included managed pine plantations, mixed pine-hardwood communities, and bottomland hardwood communities (Workman and McLeod 1990). Pine plantations consist of monocultures of loblolly *(Pinus taeda),* slash *(P. elliotti),* or longleaf *(P. palustris)* pine depending on site quality and management objective. Natural mixed pine-hardwood communities occur throughout the site on mesic, upland sites, and along upland riparian zones and are dominated by loblolly pine, sweetgum *(Liquidamber styraciflua),* water oak *(Quercus nigra),* and red maple *(Acer rubrum).* Extensive bottomland hardwood communities associated with the Savannah River are dominated by laurel *(Q. laurifolia),* swamp chestnut *(Q. michauxii),* and cherrybark oak *(Q. pagodaefolia),* sweetgum, American elm *(Ulmus american),* tupelo gum *(Nyssa aquatica),* and bald cypress *(Taxodium distichium).* Wetland and other aquatic habitats such as beaver *(Castor canadensis)* ponds, Carolina bays, abandoned farm ponds, and impoundments are common on the SRS.

We captured evening bats in summers 1996 and 1997, and red bats and Seminole bats in summer 1997, in mist nets over streams, beaver ponds, Carolina bays, and road ruts. Species, sex, age (Anthony 1988), reproductive condition (Racey 1988), mass, and forearm length were recorded. We attached 0.5-g radiotransmitters (LB-2, Holohil Systems, Woodlawn, Ontario, Can.) between the scapula using Skin Bond® surgical cement (Pfizer Hospital Prod. Group, Inc., Largo, Fla.). Transmitter mass was ≤5% of the mass of eastern red and Seminole bats, and ≤5.5% of the mass of evening bats as recommended by Aldridge and Brigham (1988).

We used Advance Telemetry Systems R2000 receivers (Isandi, Minn.) and 3-element Yagi antenna to locate roosts (Menzel et al. 1998). Roosts were located daily following capture and continued until the transmitter was shed or the battery failed. The locations of the roosts within a tree were confirmed by conducting emergence counts at dusk.

We sampled vegetation and habitat variables in 10-m radius circular plots centered on each roost to assess roost-tree characteristics and habitat factors influencing roost tree selection by eastern red, Seminole, and evening bats. Variables measured within plots included: number of woody stems in understory, number of stems in overstory, mean height of overstory, basal area of overstory, species richness, diversity, and evenness of understory and overstory, percent canopy density, prevalence of (% of overstory trees containing) Spanish moss, and percentage of total basal area of pine trees and snags. We also measured height and dbh of roost tree, difference between average height of canopy and height of roost tree, and height of roost. Trees with dbh >9.5 cm were considered overstory. We measured overstory, roost tree, and roost height using a clinometer. Overstory dbh was measured using diameter tape. We used number of stems of each species in understory and basal area of species in the overstory to calculate Shannon's measure of diversity and Pielou's measure of evenness (Pielou 1966). Canopy density was estimated by averaging the readings taken from a spherical densiometer (Lemmon 1956) 2 m from the roost tree in each of 4 cardinal directions. The methods used in vegetation sampling of the roost trees were repeated exactly for the random trees.

We compared characteristics of the roost trees and areas surrounding roost trees of each bat species to the characteristics of 30 random trees and surrounding sites located within the study area using a Wilcoxon 2-sample test (SAS Inst. 1990). Locations of trees randomly selected were determined by randomly generating UTM coordinates using a GIS coverage of the study site. The overstory tree nearest each set of randomly generated UTM coordinates was used in the comparison. We used a log-likelihood ratio test to determine if the number of each tree species used as roosts by each species differed from expected based on the relative availability of each tree species in the study area (Sokal and Rohlf 1995). We determined relative abundance of each overstory tree species in the study area by comparing abundance of each tree species in the 30 randomly located plots to total number of overstory trees in the random plots ($N=826$). We tested for differences in roost site fidelity among the three bat species using analysis of variance and Tukey's multiple means comparison (SAS Inst. 1990). We used $\alpha = 0.05$ as the rejection criterion for all tests.

Results

We attached transmitters to 6 eastern red bats (1 juvenile male, 2 lactating and 1 non-lactating adult females, and 2 juvenile females), 6 Seminole bats (2 adult and 1 juvenile males, and 1 adult and 1 juvenile female), and 24 evening bats (6 adult and 1 juvenile males, 7 lactating and 9 non-lactating adult females, and 1 juvenile female). Individuals often roosted in the same tree more than one night. We located eastern red bats in 55 roost trees during 66 days, Seminole bats in 65 roost trees during 104 days, and evening bats in 61 roost trees during 204 days. The average number of consecutive days of roost-tree use was 1.2 (SE = ± 0.36) by eastern red, 1.5 (± 1.09) by Seminole, and 2.8 (± 2.78) by evening bats. Roost-tree fidelity was significantly higher for evening bats than for eastern red and Seminole bats ($F = 13.30$, d.f. $= 2$, $P = 0.0001$). Roost fidelity did not differ between eastern red and Seminole bats.

Eastern red bats roosted within the canopy of older (≥40 years) hardwood trees, clinging to leaf petioles or the tips of small branches (<4 cm in diam.). Average roost height was 16 ± 3.3 m. Trees used by eastern red bats had larger dbh and were taller, extending higher above the surrounding canopy than randomly located trees (Table 1). Tree species composition used by eastern red bats as roosts differed from the relative abundance of tree species in the study area ($G = 144.5$, d.f. $= 23$, $P = 0.011$; Table 2). Although red bat roosts were found in 20 different tree species, they most commonly

Table 1. A comparison of the characteristics of 55 trees used as roosts by eastern red bats and their surroundings with 30 randomly located trees and their surroundings in the Upper Coastal Plain of South Carolina, summer 1997.

	Eastern red bat		Randomly selected			
Roost characteristic	$\bar{x}$	SE	$\bar{x}$	SE	χ^2	P
Roost tree height (m)	23.9	0.71	19.2	2.98	14.6	0.0001
Roost tree diameter (cm)	37.4	2.10	22.8	2.52	19.9	0.0001
Length above canopy (m)	6.9	0.64	3.8	2.73	14.1	0.0002
N understory	51.9	5.85	68.1	9.06	3.5	0.0624
N overstory	28.0	1.04	28.0	1.94	0.01	0.9157
Overstory height	17.0	0.34	15.4	0.67	4.5	0.0336
Basal area overstory	16,702.4	779.17	13,335.9	1,601.05	8.9	0.0029
Understory richness	9.34	0.569	8.31	0.594	1.0	0.3130
Understory diversity	1.73	0.059	1.48	0.092	6.0	0.0141
Understory evenness	0.82	0.013	0.72	0.032	4.0	0.0449
Overstory richness	9.18	0.316	5.00	0.547	30.7	0.0001
Overstory diversity	1.64	0.052	0.85	0.115	29.7	0.0001
Overstory evenness	0.75	0.018	0.58	0.046	14.0	0.0002
% canopy density	87.7	1.62	76.5	3.56	17.3	0.0001
% moss	0.7	0.45	2.1	1.30	2.0	0.1531
% conifer	11.7	3.34	51.0	7.53	21.5	0.0001
% snag	5.2	1.30	2.8	0.62	1.4	0.2295

Table 2. Comparison of the species composition of roost trees of eastern red, Seminole, and evening bats to the species composition of trees in randomly located plots in the Upper Coastal Plain of South Carolina during summer 1996, 1997.

Tree species	Eastern red bat	Seminole bat	Evening bat	Random
Acer rubrum (red maple)	10.9	1.5	1.6	1.7
Carya glabra (pignut hickory)	1.8	0.0	0.0	0.6
C. tomentosa (mockernut hickory)	5.5	0.0	0.0	1.8
Fraxinus pennsylvanica (green ash)	3.6	0.0	3.3	1.1
Liquidamber styraciflua (sweetgum)	14.5	4.6	0.0	18.9
Liriodendron tulipifera (tulip poplar)	7.3	0.0	1.6	0.0
Nyssa aquatica (water tupelo)	7.3	0.0	0.0	0.0
N. biflora (black gum)	3.6	0.0	0.0	1.1
N. sylvatica (black gum)	1.8	1.5	0.0	3.0
Pinus echinata (shortleaf pine)	0.0	1.5	0.0	0.0
P. elliottii (slash pine)	0.0	15.4	1.6	3.4
P. palustris (longleaf pine)	1.8	9.2	44.3	5.0
P. taeda (loblolly pine)	0.0	58.5	0.0	31.8
Platanus occidentalis (sycamore)	0.0	1.5	0.0	0.0
Quercus alba (white oak)	5.5	0.0	0.0	1.6
Q. durandii (Durand's white oak)	0.0	0.0	0.0	0.2
Q. falcata (southern red oak)	1.8	0.0	0.0	1.9
Q. laurifolia (laurel oak)	5.5	3.1	1.6	9.0
Q. lyrata (overcup oak)	5.5	0.0	0.0	0.0
Q. michauxii (swamp chestnut oak)	1.8	0.0	0.0	0.4
Q. nigra (water oak)	5.5	3.1	0.0	4.8
Q. phellos (willow oak)	3.6	0.0	0.0	3.4
Q. stellata (post oak)	7.3	0.0	0.0	2.1
Snag	0.0	0.0	41.0	5.0
Taxodium distichum (bald cypress)	0.0	0.0	1.6	0.0
Ulmus alata (winged elm)	3.6	0.0	0.0	0.5
U. americana (American elm)	1.8	0.0	3.3	0.1

were located in sweetgum (*Liquidamber styraciflua,* 14.5%) and red maple (*Acer rubrum,* 10.9%; Table 2). Nine (64%) of the 14 characteristics of plots surrounding roost trees of eastern red bats differed from random plots. Compared with random plots, roosts selected by eastern red bats were located in areas with higher average overstory tree height and basal area. Overstory canopy was denser around red bat roosts than in random plots. Understory and overstory diversity was higher surrounding red bat roosts than random plots. Conifers were less prevalent surrounding eastern red bat roosts than in randomly located plots.

Seminole bats primarily roosted on small branches (<4 cm diam.) in older (≥40 years) pine trees. Average roost height was 17 ± 2.2 m. Seminole bat roosts had greater dbh and were taller and extended higher above the canopy than randomly located trees (Table 3). Tree species composition selected as roosts of Seminole bats differed from the relative abundance of tree species in the study area ($G=75.5$, d.f. $=22$, $P=0.001$; Table 2). Although Seminole bat roosts were located in 10 tree species, most roosts (85.6%) were located in pines. Loblolly (58.5%) and slash (15.4%) pines were most commonly used as roosts (Table 2). Three (21.4%) of the 14 characteristics

Table 3. A comparison of the characteristics of 65 trees used as roosts by Seminole bats and their surroundings with 30 randomly located trees and their surroundings in the Upper Coastal Plain of South Carolina, summer 1997.

	Seminole bat		Randomly selected			
Roost characteristic	$\bar{x}$	SE	$\bar{x}$	SE	χ^2	*P*
Roost tree height (m)	25.0	0.48	19.2	2.98	23.0	0.0001
Roost tree diameter (cm)	42.0	1.47	22.8	2.52	31.6	0.0001
Length above canopy (m)	9.36	0.53	3.8	2.73	29.8	0.0001
N understory	55.4	4.48	68.1	9.06	2.2	0.1364
N overstory	31.0	1.33	28.0	1.94	2.1	0.1516
Overstory height	15.7	0.30	15.4	0.67	0.04	0.8449
Basal area overstory	14,610.6	497.44	13,335.9	1,601.05	4.6	0.0330
Understory richness	6.65	0.342	8.31	0.594	12.3	0.0005
Understory diversity	1.38	0.049	1.48	0.092	1.1	0.2204
Understory evenness	0.77	0.017	0.72	0.032	1.9	0.1698
Overstory richness	5.69	0.287	5.00	0.547	0.7	0.4015
Overstory diversity	1.13	0.159	0.85	0.115	0.6	0.4481
Overstory evenness	0.58	0.023	0.58	0.046	0.2	0.6614
% canopy density	73.5	1.76	76.5	3.56	3.5	0.0628
% moss	0.1	0.01	2.1	1.30	9.8	0.0017
% conifer	47.9	3.61	51.0	7.53	0.04	0.8448
% snag	4.9	0.86	2.8	0.62	3.2	0.0720

of plots surrounding Seminole bat roosts differed from randomly located plots (Table 3). Seminole bat roosts were located in areas with higher basal area and lower understory richness and less Spanish moss than in random plots (Table 3).

Evening bats roosted in tree cavities or under exfoliating bark. Average roost height was 8 ± 0.6 m. Trees used by evening bats were larger in dbh, taller, and extended higher above the surrounding canopy than randomly located trees (Table 4). Tree species composition of evening bat roosts differed from the relative abundance of tree species in the study area ($G = 225.7$, d.f. $= 22$, $P = 0.001$; Table 2). Evening bat roosts were located in nine tree species (Table 2). Most roosts were located in large longleaf pines (44.3%) or dead conifer snags in beaver ponds (41.0%; Table 2). Seven (50%) of the 14 characteristics of plots surrounding roost trees selected by evening bats differed from random plots (Table 4). Compared with random plots, evening bats roosted in areas with fewer overstory and understory trees, higher average canopy height, lower understory richness and diversity, lower overstory richness, less dense canopies, and a higher abundance of snags (Table 4).

Discussion

Despite morphologic similarity between eastern red and Seminole bats (Laerm et al. 1999), they roosted in markedly different areas of the study site. Eastern red bats roosted primarily in mature bottomland hardwood communities, whereas Seminole bats roosted in mature pine and mixed pine-hardwood communities. Differences in roost selection may reflect resource partitioning, an evolutionary adaptation to minimize interspecific competition between these 2 species (Schoener 1974).

Table 4. A comparison of the characteristics of 61 trees used as roosts by evening bats and their surroundings with 30 randomly located trees and their surroundings in the Upper Coastal Plain of South Carolina, summer 1996, 1997.

	Evening bat		Randomly selected			
Roost characteristic	$\bar{x}$	SE	$\bar{x}$	SE	χ^2	*P*
Roost tree height (m)	21.7	0.79	19.2	2.98	7.8	0.0053
Roost tree diameter (cm)	35.8	2.02	22.8	2.52	18.3	0.0001
Length above canopy (m)	4.1	0.73	3.8	2.73	5.0	0.0253
N understory	34.2	3.92	68.1	9.06	14.1	0.0002
N overstory	22.7	1.25	28.0	1.94	8.4	0.0037
Overstory height	17.6	0.54	15.4	0.67	6.7	0.0097
Basal area overstory	12,083.1	464.6	13,335.9	1,601.05	0.04	0.8394
Understory richness	5.63	0.407	8.31	0.594	12.0	0.0005
Understory diversity	1.21	0.073	1.48	0.092	3.7	0.0541
Understory evenness	0.49	0.039	0.72	0.032	1.4	0.2407
Overstory richness	3.59	0.317	5.00	0.547	4.3	0.0386
Overstory diversity	0.58	0.074	0.85	0.115	2.8	0.0929
Overstory evenness	0.49	0.039	0.58	0.046	1.0	0.3062
% canopy density	56.7	4.03	76.5	3.56	7.1	0.0007
% moss	0.8	0.35	2.1	1.30	0.9	0.3417
% conifer	50.9	6.04	51.0	7.53	0.04	0.8363
% snag	21.9	4.42	2.8	0.62	4.4	0.0352

In contrast to the foliage roosting bats, evening bats selected roosts located under exfoliating bark in mature (≥40 years) longleaf pines or within cavities located in beaver–pond snags. Suitable evening bat roost sites are maintained by contrasting environmental factors, such as regular prescribed fire and precommercial thinning in pine stands and inundation in beaver ponds. Each of these disturbances reduced surrounding overstory trees, lowered overstory and understory diversity, and lowered canopy density compared with randomly located stands.

For all 3 bat species, tree-roosts had larger diameters, were taller, and extended farther above the surrounding canopy than randomly located trees, which was not unique to SRS (Betts 1996, Crampton and Barclay 1996, Taylor and Savva 1998, Vonhof and Barclay 1996, Menzel et al. 1998). Larger trees that extend above the surrounding canopy are exposed to greater solar radiation; therefore, these roosts are possibly selected to speed fetal and juvenile bat growth and development (Racey and Swift 1981, Racey 1988). Larger and more exposed trees may benefit bats because they are easier to access and relocate after foraging, and lessen bat exposure to predation upon entering and exiting roosts (Barclay et al. 1982, Vonhof and Barclay 1996). We suspect that evening bats selected larger trees because cavities were probably more numerous than in smaller trees. Furthermore, cavities in the larger trees had thicker walls, which promote thermal stability and increased permanence (Kurta 1985).

All 3 species of bats used multiple roost trees and switched roosts regularly, similar to the findings of others (Betts 1995, Crampton and Barclay 1995, Vonhof 1996, Vonhof and Barclay 1996, Menzel et al. 1998, Menzel et al. 1999, Menzel et al.

2001). Differences in roosts between evening bats and the 2 Lasiurine bats probably are related to roost permanence and availability (Lewis 1995). Cavity roosts are more permanent but less available across the landscape than foliage roosts (Lewis 1995).

Although we lack a mechanistic understanding of roost selection choices by eastern red, Seminole, and evening bats, observed tree-roost selection may have implications for the impact of forest management on these bat species. Minimal forest management activities in bottomland hardwoods, along with maturing longleaf pine stands and continued longleaf pine restoration efforts at SRS undoubtedly will provide roosting habitat for all 3 species. Conversely, throughout much of the Upper Coastal Plain, ongoing conversion of longleaf pine forests (Landers et al. 1995), continued shortening of loblolly pine rotations (Borders and Bailey 1997), and projected removals in regional bottomland hardwood forests (Wigley and Roberts 1994) will decrease suitable roosting habitat for these bat species. Threshold levels of roost-tree availability, especially for cavity-roosting evening bats, are unknown. Accordingly, further research identifying roost-tree use and availability across a variety of southeastern landscapes and forest management regimes will be necessary for conservation of eastern red, Seminole, and evening bats.

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