Quantitative comparison of tree roosts used by red bats (*Lasiurus borealis*) and Seminole bats (*L. seminolus*)

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Abstract: We radio-tracked 11 red bats (*Lasiurus borealis*) and 5 Seminole bats (*L. seminolus*) to 64 and 34 day roosts, respectively. Individuals of both species were found roosting within the canopy of the roost trees, clinging to leaf petioles or the tips of small branches (<4 cm in diameter). Red bats roosted primarily in hardwoods (97%), whereas the roosts of Seminole bats were located primarily in pines (94%). Ten of the 16 roost-site variables examined differed significantly between red bats and Seminole bats: number of trees in the overstory, overstory height, understory richness and diversity, overstory richness, diversity, and evenness, roost-tree diameter, percent canopy closure, and percentage of conifers in the overstory. These differences were related directly to the differential use of roosting habitats by the two species. The roosts of red bats were located in pine – mixed hardwood communities and bottomland hardwood swamps, while the roosts of Seminole bats were located in communities dominated by pines. To examine within-stand roost selection, the diameter, height, and species composition of roost trees used by red and Seminole bats were compared with those of neighboring trees. Roost trees of red and Seminole bats had significantly larger diameters and were significantly taller than surrounding trees. Day roosts of red and Seminole bats were located in 18 and 5 tree species, respectively. The tree species used differed significantly from expected for the red bat but not for the Seminole bat.

Résumé : Nous avons suivi par radiotélémétrie les déplacements de 11 Chauves-souris rousses (*Lasiurus borealis*) vers 64 dortoirs de jour et de 5 Chauves-souris séminoles (*L. seminolus*) vers 34 dortoirs. Les chauves-souris des deux espèces ont été trouvées dans le feuillage des arbres des dortoirs, cramponnées aux pétioles des feuilles ou aux extrémités de petits rameaux (diamètre <4 cm). Les Chauves-souris rousses ont été trouvées surtout dans les bois durs (97%) et les Chauves-souris séminoles, surtout dans les pins (94%). Seize variables reliées aux dortoirs ont été examinées et dix d'entre elles différaient significativement chez les deux espèces : nombre d'arbres dans l'étage supérieur de la forêt, hauteur de l'étage supérieur de la forêt, richesse et diversité de l'étage inférieur de la forêt, richesse, diversité et régularité de l'étage supérieur de la forêt, diamètre des arbres de repos, densité du feuillage en pourcentage, pourcentage des conifères dans l'étage supérieur de la forêt. Les différences étaient directement reliées à l'utilisation différentielle des habitats offerts par les dortoirs chez les deux espèces. Les dortoirs des Chauves-souris rousses étaient situés dans les communautés mixtes bois durs – pins et dans les marécages bas à bois durs, alors que les dortoirs des Chauves-souris séminoles étaient situés dans les communautés dominées par les pins. Pour déterminer les préférences de sites de repos à l'intérieur d'un dortoir, le diamètre, la hauteur et la composition en espèces des arbres du dortoir utilisés par le deux espèces de chauves-souris ont été comparés aux mêmes variables des arbres avoisinants. Les arbres utilisés par les deux espèces avaient un diamètre et une hauteur significativement supérieurs à ceux des arbres avoisinants. Les dortoirs des Chauves-souris rousses comportaient 18 espèces d'arbres, ceux des Chauves-souris séminoles, 5 espèces. Chez les Chauves-souris rousses, mais pas chez les Chauves-souris séminoles, les espèces d'arbres utilisées différaient significativement de celles indiquées par les prédictions théoriques.
[Traduit par la Rédaction]

Introduction

Although bats are an important component of forest ecosystems, our understanding of their habitat requirements has lagged behind our understanding of those of other mammalian groups. Until recently, most of the information on bat roosts and roosting behavior came from observations made at caves, mines, or artificial structures (Betts 1995). Other than anecdotal accounts, little was known of roost-site selection among tree-roosting bats (e.g., Barclay and Cash 1985; Constantine 1958, 1966; Parsons et al. 1986). With the advent of miniaturized radio transmitters, more detailed analysis of chiropteran habitat preferences, roost selection, and roosting behavior is possible (see Barclay et al. 1988; Lunney et al. 1988; Taylor and Savva 1988; Vonhof 1995). It is now feasible to compare roost-site selection between closely related species in the same locale (Lacki 1995).

In eastern North America, few details are known about the characteristics of tree roosts used by two related species, the red bat (*Lasiurus borealis*) and the Seminole bat (*L. seminolus*). Based upon anecdotal accounts, red bats are assumed to commonly roost in foliage at the edge of hardwood tree canopies (Barbour and Davis 1969; Constantine 1966; Koontz

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and Davis 1991; McClure 1942; Mumford 1973). Their roosts may also be located in clumps of Spanish moss (*Tillandsia usneoides*; Constantine 1966; Jennings 1958), in coniferous trees (McClure 1942), in woodpecker holes (Fassler 1975), and under sunflower (*Helianthus* sp.) leaves (Downes 1964). Seminole bats often roost in Spanish moss (Barbour and Davis 1969; Constantine 1958; Harper 1927; Jennings 1958; Wilkins 1987). They may also occupy clumps of foliage (Sealander and Heidt 1990), tree branches (Barkalow and Adams 1955), the tips of pine limbs (M.A. Menzel et al., in preparation),[3] and cavities under loose bark (Sealander 1979). Destruction of roosts may be the most important factor in the decline of bat populations in North America (Kunz 1982). Because red bats and Seminole bats spend more than half of each day in forest roosts (Kunz 1982; Vonhof and Barclay 1996), conservation of these species may depend in part on a detailed knowledge of their roost-site characteristics. Since these two species are closely related, it is often assumed that their roost locations are similar within a limited geographic range. Since studies of related species in the same locale are valuable for identifying interspecific differences in roost-site selection (Betts 1995), we compared the characteristics of roost trees used by the red bat and Seminole bat in two locations with similar forest characteristics.

Methods

Study areas

We conducted this study during June and July 1995 and from June to August 1996. The study was conducted on Sapelo Island, Georgia, in 1995 and at the Savannah River Site National Environmental Research Park, South Carolina, in 1996. Sapelo Island is a 4411-ha barrier island located approximately 63 km south of Savannah, Georgia, and 5.5 km off the coast (31°27′N, 81°16′W). The Savannah River Site is a 76 900-ha National Environmental Research Park administered by the United States Department of Energy. It is located 23 km southeast of Augusta, Georgia (33°15′N, 81°40′W). Communities of longleaf pine (*Pinus palustris*), loblolly and slash pine (*P. taeda* and *P. elliottii*, respectively) and pine – mixed hardwoods were common to both sites. Pond pine (*P. serotina*) communities and maritime oak forests dominated by live oaks (*Quercus virginiana*) were found only on Sapelo Island. Bottomland communities were restricted to the Savannah River Site.

Roosting sites

Bats were captured in mist nets set up over small ponds or creeks or along trails. The species, sex, mass, forearm length, and age of all bats captured were recorded. Individuals were separated into juvenile and adult age-classes based on the degree of epiphyseal–diaphyseal ossification (Anthony 1988).

Roost trees were located using standard radiotelemetric techniques. We attached LB-2 radio transmitters (0.46 g; Holohil Systems Ltd., Woodlawn, Ontario) to 11 red bats and 5 Seminole bats. Transmitters were attached between the scapulae of the bats with Skin Bond® surgical adhesive (Pfizer Hospital Products Group, Inc., Largo, Florida). The fur was not clipped prior to attachment of the transmitters. Transmitter load was less than 5% of the animal's mass (Aldridge and Brigham 1988). Radio-tagged bats were located during the day using Advanced Telemetry System R2000 receivers (Isanti, Minnesota) and three-element Yagi antennas. When roost trees could not be reliably identified using radiotelemetry, roost locations were verified using binoculars during the day or by watching the roost for emerging bats at dusk. We conducted exit counts on 24 roost trees of red bats and 16 roost trees of Seminole bats. For roost trees on which exit counts were conducted, 23 (96%) and 14 (87%) used by red bats and Seminole bats, respectively, were correctly identified using radiotelemetry. In the three cases where the roost tree was incorrectly identified using radiotelemetry, the actual roost tree was within 2 m. In all three cases, the roost tree identified using radiotelemetry differed by less than 3 m in height and 15 cm in diameter from the actual roost tree, and was of the same species as the actual roost tree. All bats were tracked as long as the transmitter remained operational and attached to the bat. Average transmitter life was 14 days. Transmitters remained attached to the bats for an average of 8 days.

After a roost tree was located it was marked with flagging. Between 2 and 14 days after the roosting site was located, quantitative measurements were taken on the roost tree and the vegetation surrounding it. A 0.04-ha sampling plot (radius 11.35 m) was established around the roost tree. The diameter at breast height (DBH), height, and species of all overstory trees (DBH >9 cm) within the plot were measured. The species and stem number of all trees in the understory were recorded. Measurements taken on the roost tree included DBH, total height, and height to the base of the live crown. All heights were measured using a clinometer. Percent canopy closure was measured for each plot using a spherical densiometer (Forest Densiometers, Arlington, Virginia). We measured the density of the canopy 2 m from the base of the roost tree on the side of the tree on which the bat was roosting. Measurements were taken in the four cardinal directions and the mean density was recorded. The aspect of the roost and the height of the bat in the tree were also recorded. We measured aspect using a compass and corrected to true north. Shannon's diversity index and Pielou's measure were calculated for both the overstory and understory vegetational communities surrounding the roosts (Pielou 1966). Measures of basal area were used in calculating all overstory indices. Understory calculations are based on the number of stems per 0.04-ha sampling plot.

The heights and DBHs of roost trees used by red and Seminole bats were compared with the average height and diameter of all overstory trees within the sampling plots. The average height and DBH of all overstory trees surrounding the roost tree within each 0.04-ha sample plot were calculated. The average height and DBH of all trees surrounding the roost trees of red bats were compared with the average height and DBH of all trees used as day roosts by red bats. The average height and diameter were also calculated for all trees surrounding the roost trees of Seminole bats and the same comparisons were made. The use of each tree species as a day roost was compared with the abundance of each species within the sample plots.

We determined the universal transverse mercator (UTM) coordinates of all roost trees using a Trimble Pathfinder global positioning system (GPS). Final coordinates were obtained using differential correction. We calculated the roost area of five adult red bats and four adult Seminole bats using the minimal convex polygon method and the program calhome (Kie et al. 1996). The roosting area calculated for each individual was the area of a minimal convex polygon that included all roost trees used by the individual while it was being tracked. Roosting areas were compared between adult red bats and Seminole bats using a two-sample t test (SAS Institute Inc. 1990).

We tested for differences in all roost characteristics between roosts located on Sapelo Island and at the Savannah River Site using a two-sample t test. No significant differences were detected, therefore data collected at both sites were pooled for all analyses.

We compared 16 characteristics of day-roost sites between red bats and Seminole bats by means of a two-sample t test. The aspects of roosts selected by red and Seminole bats were compared with those expected on the assumption of a random distribution, using a

[3] M.A. Menzel, D.M. Krishon, T.C. Carter, and J. Laerm. Notes on tree roost characteristics of the northern yellow bat (*Lasiurus intermedius*), the Seminole bat (*L. seminolus*), the evening bat (*Nycticeius humeralis*), and the eastern pipistrelle (*Pipistrellus subflavus*).

Table 1. Comparison of 16 roost-site characteristics between *Lasiurus borealis* and *L. seminolus*.

Roost-site characteristic	*L. borealis*	*L. seminolus*	*P*
No. of trees in understory	42.0±3.92	45.6±9.03	0.7161
No. of trees in overstory	23.9±0.89	17.9±1.57	0.0006
Height of overstory (m)	17.3±0.49	21.1±0.73	0.0001
Basal area of overstory (m^2/ha)	35.3±2.17	35.2±2.36	0.9767
Richness of understory	6.9±0.33	3.7±0.39	0.0001
Diversity of understory	1.4±0.06	0.8±0.09	0.0001
Evenness of understory	0.7±0.02	0.6±0.05	0.0760
Richness of overstory	6.5±0.29	3.1±0.32	0.0001
Diversity of overstory	1.3±0.04	0.5±0.90	0.0001
Evenness of overstory	0.7±0.02	0.4±0.06	0.0001
Diameter of roost tree (cm)	38.0±2.24	43.6±1.69	0.0510
Height of roost tree (m)	25.0±0.99	27.8±1.03	0.0762
Roost height (m)	15.3±1.87	16.3±1.03	0.6432
Percent canopy closure	92.3±0.76	68.5±3.68	0.0001
Percentage of snags in overstory	2.6±0.01	2.0±0.01	0.6097
Percentage of conifers in overstory	19.7±0.03	82.9±0.04	0.0001

Note: Values are given as the mean ± SE.

likelihood-ratio test (Sokal and Rohlf 1969). To examine within-stand roost selection, we compared the heights and DBHs of roost trees used by red and Seminole bats with the average height and DBH of surrounding trees using a two-sample *t* test. The number of times a tree of a particular species was used as a roost was compared with the abundance of that species within the sampling plots, using a χ^2 test..

Table 2. Proportion of each species of tree used for roosting compared with the abundance of that species within the 0.04-ha sampling plot surrounding the roosts of *Lasiurus borealis* and *L. seminolus*.

	L. borealis		*L. seminolus*	
Tree species	Roosting	Random	Roosting	Random
Acer leucoderme	1.6	0.1	0	0
A. rubrum	1.6	4.7	0	0
Carya glabra	1.6	0.9	0	0
Liquidamber styraciflua	24.6	25.2	0	0
Liriodendron tulipifera	4.9	6.0	0	0
Nyssa aquatica	3.4	5.6	0	0
N. sylvatica	8.3	7.0	0	0
Platanus occidentalis	1.6	0.4	0	0
Quercus alba	9.8	4.8	0	0
Q. durandii	3.4	0.2	0	0
Q. falcata	1.6	0.6	0	0
Q. michauxii	1.6	1.4	0	0
Q. laurifolia	8.3	9.6	0	0
Q. nigra	21.3	15.1	0	0
Q. stellata	1.6	1.1	0	0
Q. virginiana	0	0	5.6	3.0
Ulmus americana	1.6	2.3	0	0
Pinus palustris	1.6	0.8	13.9	10.7
P. taeda	1.6	14.2	30.5	25.4
P. elliottii	0	0	47.2	55.6
P. serotina	0	0	2.8	5.3

Results

We tracked 11 red bats and 5 Seminole bats to their day roosts. The 64 roost trees of red bats were used on 74 nights, the 34 roost trees of Seminole bats on 57 nights. Average roost-site fidelity for red and Seminole bats was 1.2 and 1.7 nights per roost tree, respectively.

Radio transmitters were placed only on Seminole bats captured at the south end of Sapelo Island. Although over half (54%) of the study area on Sapelo Island consisted of hardwood-dominated communities, 25 roosts of Seminole bats (88%) were located in communities dominated by pines. While the Savannah River Site study area contained primarily pine-dominated communities (74%), 55 roost trees of red bats (86%) were located in hardwood communities. At the Savannah River Site, all nine (100%) of the roosts of Seminole bats were located in pine-dominated communities. Ten of the 16 roost-site characteristics examined differed significantly between red and Seminole bats (Table 1). The 0.04-ha sampling plots surrounding the roosts of red bats contained more overstory trees (mean ± SE = 23.90 ± 0.89) than the plots surrounding roosts of Seminole bats (17.94 ± 1.57). The overstory surrounding the roosts of Seminole bats (21.1 ± 0.7 m) was significantly higher than that surrounding the roosts of red bats (17.3 ± 0.5 m). Roost-tree diameters also differed between the two species. The average DBH of red bat roost trees (38.0 ± 2.2 cm) was significantly smaller than that of Seminole bat roost trees (43.6 ± 1.7 cm). Both the overstory and the understory surrounding the roosts of red bats showed greater richness and diversity than those surrounding the roosts of Semi nole bats (Table 1). The percentages of conifers in the over story also differed significantly between the roosts of red an Seminole bats. On average, 20% of overstory trees surround ing the roosts of red bats were conifers. In contrast, the over story surrounding the roosts of Seminole bats consisted, o average, of 83% conifers. Percent canopy closure surroundin the roosts of red bats (92.3 ± 0.8%) was significantly highe than around the roosts of Seminole bats (68.5 ± 3.7%).

Red bats were found roosting in 18 species of trees (Table 2 Sweetgums (*Liquidamber styraciflua*), black gums (*Nyssa sy vatica*), white oaks (*Quercus alba*), laurel-leaved oak (*Q. laurifolia*), and water-oaks (*Q. nigra*) were commonl used. The species composition of roost trees differed signif cantly from the composition expected in hardwood habitat assuming random selection of tree species within the roostin area (G = 29.25, P = 0.03). Red maples (*Acer rubrum*) an loblolly pines commonly occurred within the roost plots; how ever, each species was used only once as a day roost. Whi oaks and water-oaks occurred infrequently within the roo plot, but both species were commonly used as day roos (Table 2). Both DBHs and heights of roost trees used by re bats were significantly greater than the average DBH ar height of surrounding trees (Table 3). The roost aspects s lected did not differ significantly from a random distributio

Seminole bats were found roosting in five species of tre (Table 2). Loblolly pines, slash pines, and longleaf pines we commonly used. The species composition of roost trees did n

Table 3. Comparison of the diameters and heights of trees used as roosts by *Lasiurus borealis* and *L. seminolus* with the average diameter and height of all overstory trees within the 0.04-ha plots surrounding the roosts.

	L. borealis			*L. seminolus*		
	Roost	Random	*P*	Roost	Random	*P*
DBH (cm)	37.75±2.22	22.53±0.70	0.0001	42.08±1.84	30.18±1.27	0.0001
Height (m)	24.85±1.00	16.96±0.48	0.0001	26.51±1.07	20.72±0.72	0.0001

Note: Values are given as the mean ± SE.

iffer significantly from the expected composition within ine-dominated habitats. Like red bats, Seminole bats roosted 1 trees of greater heights and DBHs than the average values or trees within the roost plot (Table 3). Roosting sites were elected randomly with respect to aspect.

Roosting areas differed significantly between red and Semi-ole bats. Both species moved to new roost trees often. Red ats and Seminole bats spent an average of 1.2 and 1.7 days n one roost tree, respectively. While individuals of both spe-ies often moved to new roost trees, adult red bats selected oosts within a significantly larger area (2.6 ± 0.6 ha) than dult Seminole bats (0.2 ± 0.1 ha; $P = 0.01$).

)iscussion

'he differences between the roosting sites of red and Seminole ats were related directly to the different roosting habitats used y the two species. The roosts of red bats were located both in ine – mixed hardwood communities dominated by sweet-ums, water-oaks, and loblolly pines and in bottomland hard-vood swamps dominated by cotton-gum (*Nyssa aquatica*) and ald cypress (*Taxodium distichum*). The roosts of Seminole ats were always located in forest communities dominated by ines. Both on Sapleo Island and at the Savannah River Site, ine-dominated communities are intensively managed for the roduction of forest products. Stands of pines were typically omposed of a single tree species and all individual trees were f approximately the same age and size. The understory com-nunities surrounding the roosts of Seminole bats were man-ged with the use of prescribed fires, resulting in a open nderstory or shrub communities dominated by a few fire-dapted species. The understory communities surrounding the oosts of Seminole bats were less diverse than those surround-1g the roosts of red bats. The pine – mixed hardwood commu-ities and bottomland hardwood swamps where red bats oosted were managed much less intensively. These stands 'ere not thinned. Because red bats roosted in less intensively ıanaged stands, their roosts were surrounded by more over-tory trees than those of Seminole bats. Since there were more ees in the overstory, canopy density surrounding the roosts of ed bats was greater than that surrounding the roosts of Semi-ole bats. Because of the uneven-aged overstory in the less ntensively managed stands, average overstory heights were ower and average roost-tree diameters smaller for red bats ıan for Seminole bats.

Except for their height in the tree, the roosts of red bats were imilar to those described in the literature. We found red bats oosting at an average height of 15.3 m, higher than those ound by Mumford (1973; 2.6 m), Koontz and Davis (1991; .5 m), and McClure (1942; 1.6–12.5 m). Previous investiga-ons into the roosting habits of red bats involved visually lo-cating the roosts. Bats roosting lower in the tree may be located more easily by visual searches than those roosting high in the canopy (Mumford 1973). Because we located our roosts by means of radiotelemetry, our estimates of roosting heights are probably more representative than previous estimates. Like McClure (1942) and Constantine (1966), we found red bats roosting in many species of trees. Although McClure (1942) compared the proportions of roosts located in different species of trees with the relative abundance of each tree species, he did not determine if any tree species were used more often than expected. We found that red bats preferred white oaks and water-oaks and did not roost in red maples or loblolly pines as often as expected.

The roosts of Seminole bats that we found were unlike those previously described. Constantine (1958) found Seminole bats roosting at an average height of 2.5 m, but we found them roosting at an average height of 16.3 m. Roosts of Seminole bats were commonly located in Spanish moss (Barbour and Davis 1969; Constantine 1958; Harper 1927; Jennings 1958; Wilkins 1987). Although Seminole bats forage in pine-domi-nated communities (Harper 1927; Ivey 1959; Jennings 1958; Moore 1949; Zinn 1977), we could find no reports of Seminole bats roosting in pines. The Seminole bats we tracked almost always roosted in pines. Constantine (1958) searched for roosts of Seminole bats in Spanish moss from February through June. He located bats in every month except May and June. Jennings (1958) collected roosting Seminole bats from Spanish moss throughout the winter, but failed to collect any during July, August, or September. Jennings examined Span-ish moss for bats throughout the year, but few litters of Semi-nole bats were found. Thus, during the period of parturition and lactation, Seminole bats may commonly roost in pines. Many species of bats use different types of roost during the year in response to differing physiological demands (e.g., hibernation, pregnancy, lactation; Barbour and Davis 1969). Thus, the differences between the roosts we located and those previously described likely relate to the time of the year.

Constantine (1958, 1966) suggested that red bats and Semi-nole bats select roosts on the southwestern and southern side of roost trees, respectively. We found that the roosts of both species were selected randomly with respect to aspect.

Comparisons between the size of trees used as roosts by red bats or Seminole bats and the average size of surrounding trees in the overstory are lacking. However, Vonhof and Barclay (1996) made general comparisons between trees used as roosts by four species of bats in British Columbia and trees selected randomly from the overstory. The trees used as roosts were significantly taller than randomly selected trees. Roost trees selected by four species of bats in Tasmania had larger diame-ters than randomly selected trees (Taylor and Savva 1988). We found that roost trees used by red and Seminole bats were significantly taller and had larger diameters than surrounding trees. Our results support the findings of Vonhof and Barclay (1996) and Taylor and Savva (1988).

Adult red bats possibly select roosts from larger areas than adult Seminole bats because of the relative availability of the habitat types in which they preferred to roost. On both of our study sites, pine – mixed hardwood communities were more abundant than stands composed only of pine. The roosts of Seminole bats were found in islands of pine monoculture surrounded by pine – mixed oak communities. Seminole bats had to either restrict shifts in roost location to other trees with the island or make major shifts to different islands. Because the type of roosting habitat preferred by red bats was fairly ubiquitous, they were free to select roosts from larger areas than Seminole bats.

These data on the roosting habits of Seminole bats raise new questions concerning the effects of summer timber-harvesting operations in the southeastern United States on the reproductive success of this species. Future studies investigating the response of Seminole bats to timber harvesting in upland pine stands are needed.

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