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SEASONAL AND MULTIANNUAL ROOST USE BY RAFINESQUE'S BIG-EARED BATS IN THE COASTAL PLAIN OF SOUTH CAROLINA

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Abstract—Little is known about factors affecting year-round use of roosts by Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) or the long-term fidelity of this species to anthropogenic or natural roosts. The objectives of this study were to test whether seasonal use of roosts by Rafinesque's big-eared bats varied with roost type and environmental conditions within and among seasons and to document multiannual use of natural and anthropogenic structures by this species. We inspected 4 bridges, 1 building, and 59 tree roosts possessing basal cavity openings; roosts were inspected at least once per week from May through October in every year from 2005 through 2008 and once a month from November through April in every year from 2005 through 2009. We found that use of anthropogenic roosts was significantly greater than the use of tree roosts in summer but that the use of structure types did not differ in other seasons. There was significant seasonal variation in use of anthropogenic and tree roosts. Anthropogenic roost use was higher in summer than in all other seasons. There was no significant difference in tree use among spring, summer, and fall, but use in winter was significantly lower in 2 years of the study. Overall use of anthropogenic and tree roosts was positively related to minimum temperature, but the relationship between use of roosts and minimum temperature varied among seasons. Bats showed multiannual fidelity (≥ 4 years) to all anthropogenic roosts and to some tree roosts, but fidelity of bats to anthropogenic roosts was greater and more consistent than to tree roosts. Our data indicate that Rafinesque's big-eared bats responded differently to environmental conditions among seasons; thus, a variety of structure types and characteristics are necessary for conservation of these bats. We suggest long-term protection of roost structures of all types is necessary for conservation of Rafinesque's big-eared bats in the southeast Coastal Plain.

INTRODUCTION

Day roosts are integral to the ecology and evolution of bats, and many aspects of roost use and selection have received attention over the past two decades (Barclay and Kurta 2007, Carter and Menzel 2007, Kunz and Lumsden 2003). Studies have concentrated on habitat factors affecting roost site selection (Kalcounis-Ruppell and others 2005, Lacki and Baker 2003), effects of microclimate and parasites on roost selection (Kerth and others 2001, Reckardt and Kerth 2007, Willis and Brigham 2005), and roost fidelity (Gumbert and others 2002, Kurta and Murray 2002, Trousdale and others 2008). However, most of these studies have been conducted during the summer, and, for most temperate and boreal bat species, little is known about use of tree roosts during other times of the year (although see Boyles and Robbins 2006, Hein and others 2005, Mormann and Robbins 2007).

Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) that inhabit bottomland hardwood forests and their environs roost in large hollow trees and anthropogenic structures such as buildings, bridges, and wells (Bennett and others 2008; Carver and Ashley 2008; Gooding and Langford 2004; Lance and others 2001; Trousdale and Beckett 2004, 2005). Most studies have either examined use of anthropogenic structures or natural roosts, and few studies compare the use of anthropogenic and natural structures in a study area. Thus, it is unknown whether bats prefer one type of structure over the other or whether their preference varies seasonally.

Some studies have examined year-round roost use by Rafinesque's big-eared bats. In Louisiana and Mississippi, use of bridges as day roosts declines in winter (Ferrara and Leberg 2005b, Trousdale and Beckett 2004). Use of trees with basal openings or trees with basal and chimney openings also declines in winter in Louisiana, and bats appear to move to trees with chimney-only openings, particularly during periods of below freezing temperatures (Rice 2009). Trees with chimney-only openings have more stable temperatures, suggesting that thermal considerations may be important in selection of winter roost sites. Winter flooding may block the entrances to trees with basal openings, which may be another reason that the bats in winter select trees with chimney-only openings even though such trees provide less shelter from rain.

Multiannual roost use is another important aspect of roosting ecology. Long-term use of tree roosts appears to be related to roost type (cavity/crevice versus bark) and decomposition state of the tree. For example, bats that roost between the bark and bole of snags are less likely to reuse roosts in subsequent years than bats that roost in crevices or cavities in live-damaged trees (Barclay and Brigham 2001, Chung-MacCoubrey 2003, Lučan and others 2009, Willis and others

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2003). Further, bats that roost in relatively permanent roosts such as caves or mines show greater fidelity to their roosts than bats that use relatively ephemeral roosts such as trees (Lewis 1995). While there are a few anecdotal accounts of multiannual use of anthropogenic roosts by Rafinesque's big-eared bats (Clark 1990, Jones and Sutkus 1975), there are no quantitative data on long-term fidelity to either anthropogenic or tree roosts.

The objectives of our study were to test whether seasonal use of roosts by Rafinesque's big-eared bats varied with roost type (anthropogenic versus tree) and environmental conditions, both within and among seasons, and to document multiannual use of natural and anthropogenic structures by this species. We hypothesized that use of anthropogenic roosts and tree roosts with basal or basal-plus chimney openings would be positively related to ambient temperature and rainfall on an annual basis but would vary with season. We also hypothesized that multiannual use of anthropogenic structures would be greater than multiannual use of natural roosts.

METHODS

Our study was conducted from May 2005 through April 2009 on the U.S. Department of Energy Savannah River Site (SRS) in Aiken and Barnwell Counties, SC. The SRS is a 78 000-ha National Environmental Research Park in the sandhills and Upper Coastal Plain physiographic regions. The site is primarily forested in mid- to late-successional pine (*Pinus* spp.), mixed pine-hardwood, and upland hardwood forests (Imm and McLeod 2005). However, approximately 20 percent of SRS is swamp and bottomland hardwood forest. SRS experienced extensive disturbance and land clearing from the mid-1800s to the early 1950s when the site became Federal property (White 2005). Chief disturbances to the swamp and along the major streams prior to and after 1950 were logging, damming, high flow rates, altered temperatures from reactor cooling waters, and changes in hydrology (Kolka and others 2005). Bottomland hardwood forests consisted primarily of blackgum (*Nyssa sylvatica*), laurel oak (*Quercus laurifolia*), water oak (*Q. nigra*), red maple (*Acer rubrum*), American holly (*Ilex opaca*), sweetbay (*Magnolia virginiana*), redbay (*Persea borbonia*), ironwood (*Carpinus caroliniana*), and sweetgum (*Liquidambar styraciflua*); whereas major tree species in the swamps were water tupelo (*N. aquatica*), baldcypress (*Taxodium distichum*), and red maple. Average low and high temperatures from 1893 to 2008 ranged from 2.7 and 14.4 °C in January to 21.0 and 33.2 °C in July (Southeast Regional Climate Center, http://www.sercc.com/cgi-bin/sercc/cliMAIN.pl?sc0074). Average annual rainfall for the area was 118.4 cm (Southeast Regional Climate Center, http://www.sercc.com/cgi-bin/sercc/cliMAIN.pl?sc0074) but was below average in every year of the study (2005 to 2006, 58.3 cm; 2006 to 2007, 101.3 cm; 2007 to 2008, 106.22 cm; 2008 to 2009, 96.9 cm).

We located roosts by inspecting trees with basal cavities in bottomland forests and the surrounding areas, bridges, and old buildings and by radiotelemetry. We found trees with basal cavities during systematic searches of areas that were likely to contain potential roosts, such as mature bottomland hardwood forests and cypress-tupelo swamps, and opportunistically while conducting radiotelemetry and habitat analyses. Mature bottomland hardwood forest and cypress-tupelo swamp forests were located from forest maps, and all accessible trees within an area were examined, using a light and mirror, for the presence of Rafinesque's big-eared bats. Bats that roosted under bridges were captured by hand or with hand nets. Bats in trees with basal openings were captured by placing a mist net over the cavity entrance and capturing the bats as they emerged at dusk. All captured Rafinesque's big-eared bats were weighed, sexed, and aged and examined for parasites and injuries. We placed an aluminum lipped band (Lambournes Sophos Ltd., West Midlands, Birmingham, England) and a colored plastic split ring band (A.C. Hughes, Ltd., Middlesex, England) on the forearms of each bat. Various band placement and color combinations allowed us to determine the identity of bats when observed in a roost if the bands were visible. Capture and handling procedures followed guidelines established by the American Society of Mammalogists (Gannon and others 2007) and were approved by the Clemson University Institutional Animal Care and Use Committee (protocol numbers 50057 and ARC2008-027).

To obtain additional roost locations, we attached radio transmitters (0.42 g; Holohil Systems Ltd, Ontario, Canada) to the dorsal surface of 49 bats with Skin Bond adhesive (Pfizer Hospital Products Group, Inc., Largo, FL). We held bats for ≥ 20 minutes before releasing them to ensure the transmitter was secure. On the following and subsequent days, we used three- or five-element Yagi antenna and receiver (Wildlife Materials, Inc., Murphysboro, IL) to track bats to day roosts. If the bat was tracked to a bridge or building, the bat's relative location within the structure was recorded. If the bat was tracked to a tree, the tree was flagged, marked with a numbered aluminum tag, and identified to location with a global positioning system device. We treated tree roosts identified during random or systematic searches in the same manner. We verified that trees discovered using telemetry were the actual roost by visual inspection of the cavity with a light and mirror or by observing emergence of the bat from the cavity at dusk.

After identifying roosts, we monitored them throughout the rest of the study with the exception of roosts with only an upper bole opening or those that could not be fully examined due to a bend in the tree or because the cavity entrance was too small. We examined each roost at least once a week from May through October and at least once a month from November through April, except in the winter of 2008 to 2009 when we examined roosts at least once a week. The number of examined roosts varied throughout the study because new roosts were continually added to the sample of roost trees, and six tree roosts broke or fell during the course of the study. Some roosts were periodically inaccessible due to high water. Trees that could not be examined regularly were not included in the analyses.

We defined seasons as spring (March and April), summer (May, June, July, and August), fall (September and October), and winter (November, December, January, and February) based on climatic conditions as well as the annual cycle of Rafinesque's big-eared bats. For example, females in this area form maternity colonies and are visibly pregnant in May, and colonies begin to break up at the end of August. Thus, May was considered a summer month and September a fall month. Further, because November temperatures, particularly minimum temperatures, were more similar to December, January, and February than to October, November was considered a winter month (fig. 1).

Temperature (°C), rainfall (mm), relative humidity (percent), and windspeed (m/second) were recorded hourly at a weather station maintained by other researchers on SRS (Coleman and others 2004). Daily maximum temperature (Tmax), minimum temperature (Tmin), average daily temperature (Tavg), minimum relative humidity (RHmin), average windspeed (WSavg), and total rainfall (Rainfall) were extracted for each day from mid-May 2005 through April 2009. Because Tmax, Tmin, and Tavg were highly correlated ($r > 0.70$), only Tmin was used in statistical models. We selected Tmin because we were particularly interested in the effects of low temperatures on winter roost use.

We used a split-split-plot approximation of a repeated measures model because both year and season were repeated in the model which presented a complex covariance structure. Under conditions of equal variances and equal pairwise correlations over time, the split-split plot is an optimal method of analysis (Littell and others 1998) and is valid under the Huynh-Feldt condition which is less stringent than equal variances and covariances. We used the PROC GLIMMIX procedure (Schabenberger 2005) in SAS (2003) to fit a generalized linear mixed model to the binary (absence = 0, presence = 1) data under the binomial distribution and logit link function, resulting in a logistic response model. A three-phased approach was used to analyze relationships between roost use (0, 1) and independent variables. In phase 1, we analyzed roost use using a split-split-plot design to test fixed effects of roost type (main plot), year (split plot), and season (split-split plot) and their two- and three-way interactions. In phase 2, we tested the effects of season and year separately for each roost type using a split-plot design because we found strong interactions in the phase 1 analysis between roost type and season ($P = 0.0239$) and year and season ($P = 0.0003$). In phase 3, we modeled the effects of environmental parameters on roost use for each roost

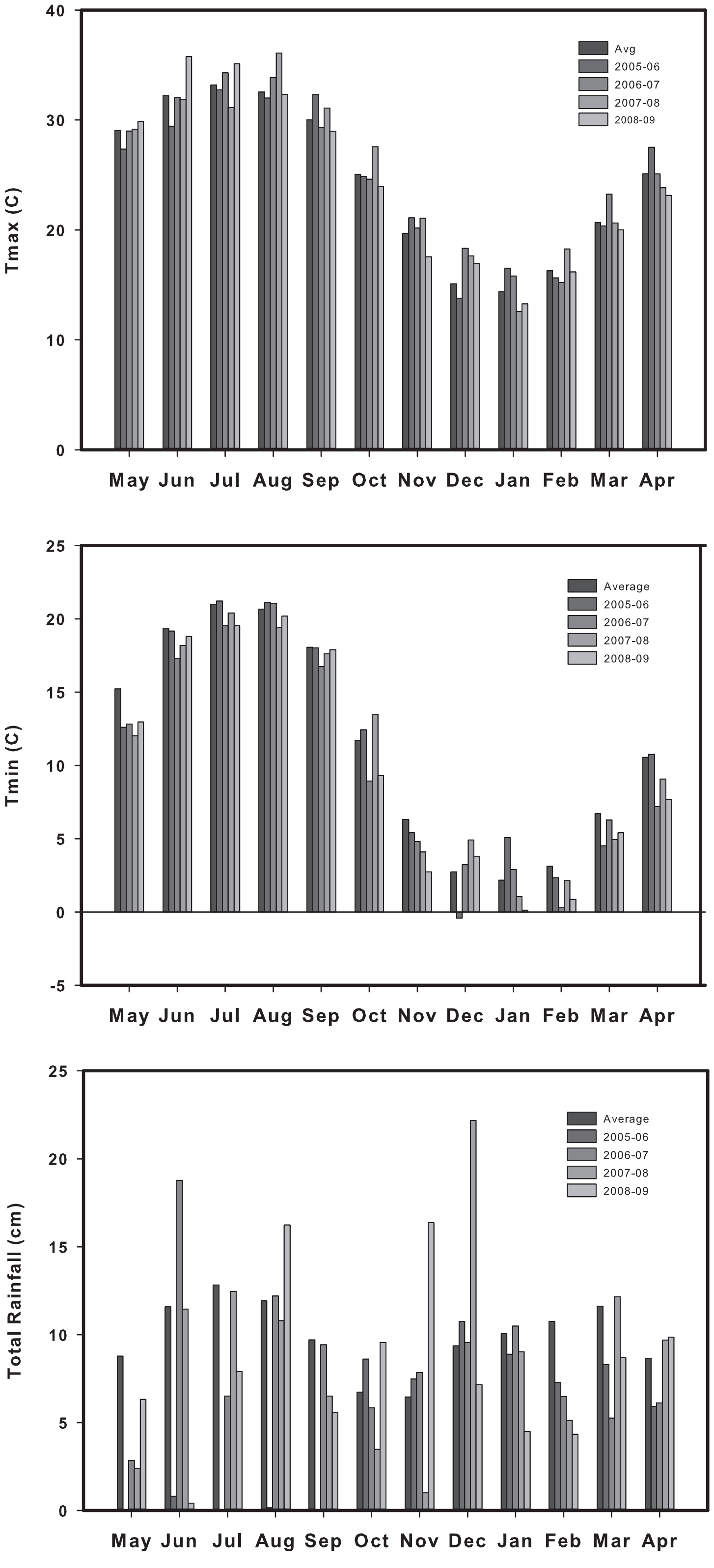


Figure 1—Long-term average (1893 to 2008) mean monthly maximum daily temperatures (Tmax), mean minimum daily temperatures (Tmin), and total rainfall (Rainfall) for the Savannah River Site, SC, and the mean maximum daily temperatures (Tmax), mean minimum daily temperatures (Tmin), and total rainfall (Rainfall) for each year of the study (2005 to 2009).

type by testing the effects of year, season, year*season, and the environmental covariates consisting of Tmin, RHmin, WSavg, Rainfall, and their interaction with season (that is, season*Tmin, season*RHmin, season*WSavg, and season*Rainfall). Homogeneity of the slope parameter over season for each of the four environmental covariates was tested by inspection of the covariate*season interactions and then reducing the full model by deleting the most nonsignificant covariate*season interaction. The reduced model was then refitted, the remaining covariate*season interactions inspected and deleted sequentially until all remaining covariate*season interactions were significant at the 0.05 level. Then this model was reduced sequentially by deleting the most nonsignificant covariate and then refitting and testing the remaining covariates until all remaining covariates were significant at the 0.05 level. For each of the final reduced models, significant covariate interactions with season indicated that the covariate slopes differed among the seasons. We used contrasts to determine which slopes were significantly different. The Bonferroni correction for each set of six pairwise comparisons among the seasonal slopes set the rejection level at $\alpha = 0.0083$ to ensure that the experimentwise error rate was maintained at 0.05 (Zarnoch 2009). All other tests were evaluated at $\alpha = 0.05$, and least square means ± 1 SE are presented.

RESULTS

Fifty-nine roost trees with basal cavities and five anthropogenic roosts were examined during the study. Anthropogenic roosts were four girder-type bridges and one barn. Tree roosts were in tupelos (*N. aquatica* and *N. sylvatica*), oaks (*Q. laurifolia, Q. michauxii, Q. nigra,* and *Q. velutina*), American beech (*Fagus grandifolia*), sweetbay, sweetgum, river birch (*Betula nigra*), yellow-poplar (*Liriodendron tulipifera*), baldcypress, and sycamore (*Plantanus occidentalis*). There were a total of 5,152 roost inspections; the number of inspections per structure ranged from 2 to 195 for roost trees and 193 to 329 for anthropogenic roosts. The number of Rafinesque's big-eared bats found in a roost ranged from zero to 9 for trees and from zero to 15 for anthropogenic roosts.

Use of anthropogenic roosts was higher than tree roost use in every month except January 2008 and during most months in winter 2009 (fig. 2). Overall use of anthropogenic roosts was not significantly different from tree roost use based on the phase 1 analysis but there was a significant roost*season interaction ($F = 3.19$, $P = 0.0239$). Thus, we conducted pairwise comparisons between anthropogenic and tree roost use for each season. Anthropogenic roost use was higher than tree use in every season but the difference was only significant during summer (fig. 3).

Use of both roost types was lowest in winter, particularly November to January, but higher in other seasons (fig. 2). Roost use in winter 2006 to 2007, particularly anthropogenic roosts, did not decline as much as in other years during the winter. Although Tmax was greater in November, December, and January 2006 to 2007 than the long-term average, it was also greater than the long-term average in

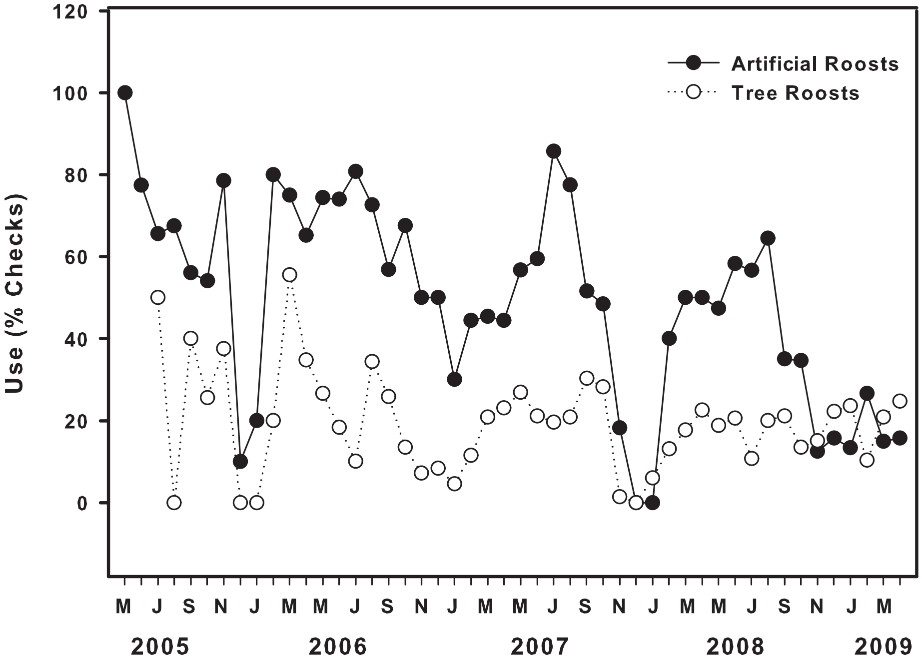


Figure 2—Percent of roost checks in which at least one Rafinesque's big-eared bat was observed in anthropogenic and tree roosts on the Savannah River Site, SC, May 2005 to April 2009.

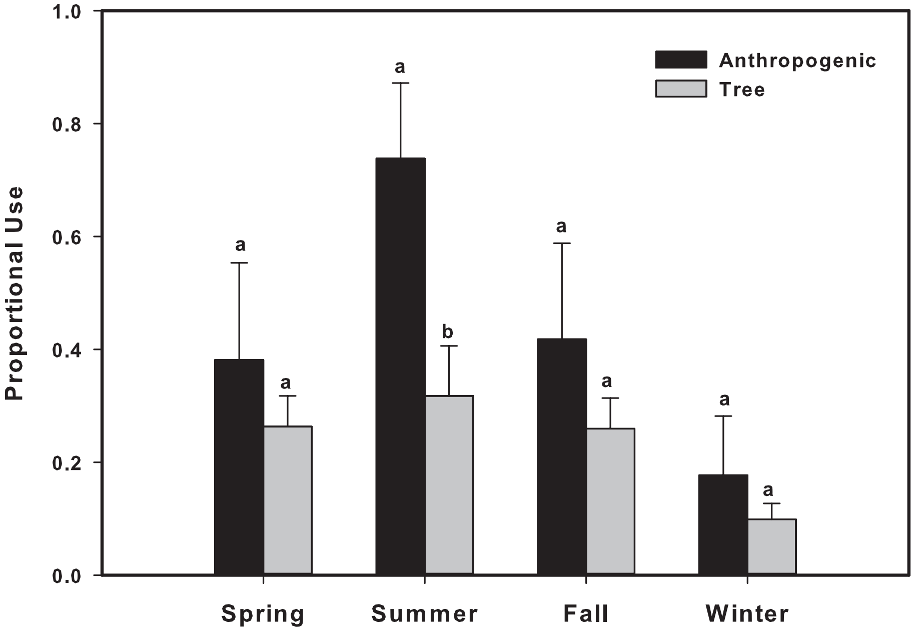


Figure 3—Mean use of anthropogenic and tree roosts by season by Rafinesque's big-eared bats on the Savannah River Site, SC, May 2005 to April 2009; means within a season with the same letter are not different ($P > 0.05$).

other years, and Tmin in 2006 to 2007 was similar to other years (fig. 1). The phase 2 analysis indicated that there was a significant interaction between year and season for both anthropogenic ($F = 2.51$, $P = 0.0192$) and tree roosts ($F = 2.02$, $P = 0.0368$). Thus, we examined seasonal use by year for each roost type. Use of anthropogenic structures was significantly greater in summer than in all other seasons in 2006 to 2007 and 2008 to 2009 and significantly greater in summer than in fall and winter in 2005 to 2006 and 2007 to 2008 (table 1). Tree roost use did not vary significantly among seasons in 2005 to 2006 and 2006 to 2007 but was significantly lower in winter than all other seasons in 2007

Table 1—Mean proportional use (± SE) of anthropogenic and tree roosts by season and year of Rafinesque's big-eared bats on the Savannah River Site, May 2005 to April 2009

Roost type	2005–06	2006–07	2007–08	2008–09
Anthropogenic roosts				
Spring	0.78±0.19^{ab}	0.36±0.23^{a}	0.47±0.28^{ab}	0.07±0.07^{a}
Summer	0.76±0.18^{a}	0.76±0.17^{b}	0.75±0.18^{b}	0.67±0.22^{b}
Fall	0.47±0.24^{b}	0.53±0.25^{a}	0.40±0.24^{a}	0.28±0.21^{a}
Winter	0.40±0.25^{b}	0.27±0.20^{a}	0.07±0.07^{c}	0.11±0.10^{a}
Tree roosts				
Spring	0.61±0.14^{a}	0.26±0.09^{a}	0.19±0.06^{a}	0.11±0.03^{ab}
Summer	0.58±0.33^{a}	0.30±0.09^{a}	0.27±0.06^{a}	0.16±0.04^{b}
Fall	0.43±0.16^{a}	0.29±0.09^{a}	0.21±0.05^{a}	0.14±0.04^{b}
Winter	0.35±0.16^{a}	0.14±0.07^{a}	0.02±0.0^{b}	0.06±0.02^{a}

[a,b,c] Proportions with the same letter within a year for a given roost type are not significantly different at the experimentwise error rate of 0.05 (Bonferroni correction, $P = 0.0083$).

Table 2—Results of phase 3 generalized linear mixed models testing the effects of environmental variables on use of anthropogenic and tree roosts by Rafinesque's big-eared bats on the Savannah River Site, SC, May 2005 through April 2009[a]

	Anthropogenic roosts				Tree roosts			
Models	Num. df[b]	Den. df[c]	*F*	*P*	Num. df[b]	Den. df[c]	*F*	*P*
Full model								
Year	3	12	2.90	0.0785	3	64	4.20	0.0089
Season	3	1199	0.13	0.9395	3	3660	3.48	0.0153
Year*Season	9	1199	2.27	0.0159	9	3660	1.52	0.1333
Tmin[d]	1	1199	20.27	< 0.0001	1	3660	4.95	0.0261
Rainfall	1	1199	0.39	0.5336	1	3660	0.60	0.4385
RHmin[e]	1	1199	12.13	0.0005	1	3660	0.23	0.6341
WSavg[f]	1	1199	2.05	0.1528	1	3660	0.21	0.6472
Tmin*Season	3	1199	4.19	0.0058	3	3660	5.57	0.0008
Rainfall*Season	3	1199	2.23	0.0828	3	3660	3.39	0.0172
RHmin*Season	3	1199	2.35	0.0712	3	3660	1.44	0.2302
WSavg*Season	3	1199	0.36	0.7808	3	3660	0.21	0.8915
Reduced model								
Year	3	12	2.67	0.0948	3	64	4.78	0.0045
Season	3	1210	3.76	0.0105	3	3738	9.09	< 0.0001
Year*Season	9	1210	2.24	0.0176	9	3738	1.71	0.0803
Tmin[d]	1	1210	16.73	< 0.0001	1	3738	5.19	0.0228
Tmin*Season	3	1210	3.71	0.0112	3	3738	5.69	0.0007
RHmin[e]	1	1210	13.70	0.0002				

[a] The full model and final reduced models are presented.

[b] Numerator degrees of freedom.

[c] Denominator degrees of freedom.

[d] Minimum temperature.

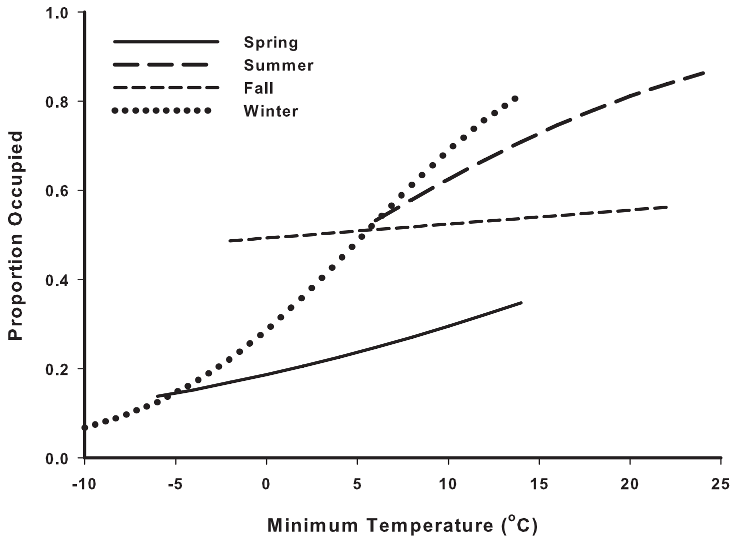
[e] Minimum relative humidity.

[f] Average windspeed.

to 2008 and significantly lower in winter than summer and fall in 2008 to 2009.

The phase 3 full model revealed use of anthropogenic roosts was significantly related to Tmin and RHmin (table 2). Anthropogenic roost use increased with increasing temperature and decreased with increasing RHmin. There was no effect of Rainfall or WSavg. However, examination of the reduced models revealed that the Tmin*season interaction was significant. The slope of use versus Tmin was significantly greater in winter than in fall ($P = 0.0018$) indicating that use was more sensitive to temperature in winter than in fall (fig. 4A). Overall, there was a significant and positive relationship between Tmin and use of tree roosts (table 2), but the interaction between Tmin and season was also significant. Use of tree roosts was positively related to Tmin in fall and winter but negatively related to Tmin in summer (fig. 4B). The effect of Tmin was significantly different ($P \le 0.0001$) between summer and fall with use decreasing with increasing Tmin in summer and increasing with temperature in fall and winter.

All five anthropogenic roosts were used in every year of study. Rafinesque's big-eared bats were present in anthropogenic roosts during 56.7 to 88.6 percent of roost checks. Of the nine trees found in year one, four were used in all years, two were used in 3 years, and three in 2 years. One of the trees used in 3 years fell in year three, and the


A) Artificial Roosts

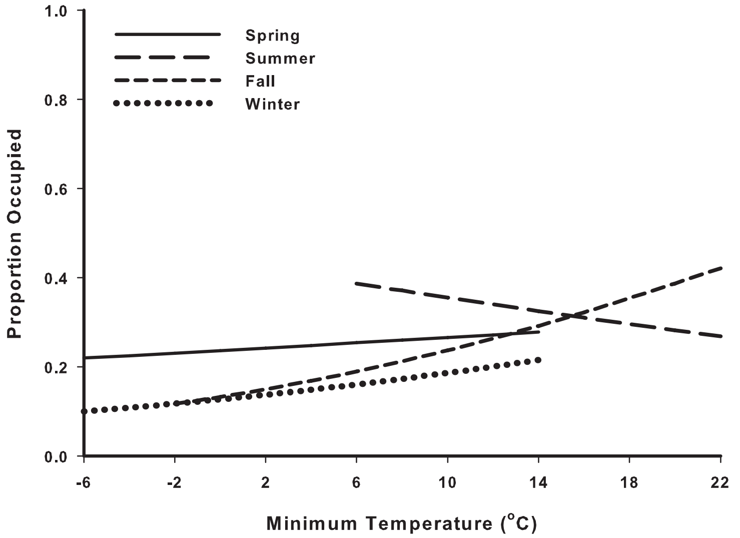

B) Tree Roosts

Figure 4—The relationship between the proportion of (A) anthropogenic roosts and (B) tree roosts occupied and minimum temperature (Tmin) for each season based on a typical year (year = 2) and typical minimum relative humidity (RHmin = 40.3 for anthropogenic roosts and RHmin = 38.1 for tree roosts) on the Savannah River Site, SC, May 2005 to April 2009. The curve segment length for each season is based on the range of minimum temperatures observed for each season and roost structure.

other was used in 2005 to 2006, 2006 to 2007, and 2008 to 2009. Of the nine trees found in year two, four were used for 3 years and five were used for 2 years; one of the trees used for 2 years fell during year four. Of the 24 trees found in year three, 15 were used in both years three and four, and 9 were only used in year three; 1 of these trees fell soon after it was discovered. The mean number of years trees were used was 3.1±0.31 for trees found in year one, 2.4±0.18 for trees found in year two, and 1.7±0.10 for trees found in year three. There was considerable variation in tree roost use across time. For trees checked ≥ 20 times, bats were present an average of 17.6 percent with a range of 1.0 to 89.2 percent.

Long-term use of roosts was accomplished by the same individual or group of individuals which was particularly evident for anthropogenic roosts. For example, orange 18 was captured and banded at bridge 603-01G in July 2003, prior to the initiation of this study, as a juvenile and was recaptured there in June 2005, July 2006, and August and October 2007. This bat was consistently observed roosting at this bridge throughout the 4-year study period and during periodic checks in summer 2009 after the study had concluded. Another example is green 22, an adult male, who was captured at bridge 603-02G in September 2004. He was observed at this bridge throughout the 4-year study period as well as summer 2009. This bat also used tree 358 during summer and fall 2006, summer and fall 2007, and winter and spring 2008 to 2009. Bridge 603-03G was used throughout the study period by a maternity colony. The bats were first observed using this bridge in September 2004, and anywhere from 1 to 15 individuals, including young, were observed at this bridge throughout the study, as well as in summer 2009. This colony also used two roost trees from summer 2007 through summer 2009. Conversely, some roosts used for 3 to 4 years were used by a sequence of different individuals. For example, tree 352 was used by orange 40, a juvenile male when banded, in fall 2005 and summer 2006; by green 28, an adult male, in summer and fall 2007; by pink 2, a juvenile male, in fall 2007; and by blue 3, an adult male, in summer 2008.

DISCUSSION

Decreased use of bridges and trees with basal cavities as day roosts by Rafinesque's big-eared bats in winter has been previously documented in Louisiana (Ferrara and Leberg 2005b, Rice 2009) and Mississippi (Trousdale and Beckett 2004). We also found decreased use of anthropogenic and tree roosts by Rafinesque's big-eared bats on the SRS in winter, but the seasonal patterns of use varied between types of roosts. Use of anthropogenic roosts peaked in summer but, in most years, there was no difference in use among fall, winter, and spring. In contrast, use of trees with basal cavities was similar during spring, summer, and fall but declined in winter, although the decline was only significant in the last 2 years of the study. Use of anthropogenic structures was also greater than use of tree roosts in summer but not in other seasons.

Differential use of anthropogenic and tree roosts may be due to differences in the microclimate of the various structures. On an annual basis, use of both anthropogenic and tree roosts was positively related to Tmin. However, we found that the relationship between roost use and Tmin varied among roost types and seasons. Use of anthropogenic roosts was more strongly influenced, i.e., a steeper slope, by Tmin in winter than in fall, and use of tree roosts was positively related to Tmin in spring, fall, and winter but negatively related to Tmin in summer. During summer, some tree roosts with basal cavities may be too warm and bats may need to search out other types of roosts such as bridges or other tree structures. Our finding that use of anthropogenic roosts was significantly greater than use of trees in summer but not significantly different during other seasons suggests that bats indeed moved from trees to anthropogenic roosts during the warmest months. In Colorado, big brown bats (*Eptesicus fuscus*) that roost in buildings are more likely to shift to new roosts or new areas within the same roost during unusually hot periods (Ellison and others 2007). Because anthropogenic roosts are larger, there may be a greater variety of microclimates within each structure where bats can move to select the best microclimate (e.g., Clark 1990, Jones and Suttkus 1975). Rafinesque's big-eared bats may also have moved to trees with chimney-only openings in summer. Rice (2009) found that cavity temperatures of roosts that have chimney-only entrances rise more slowly with increases in ambient temperature in summer and are more stable than those with basal cavities and basal-plus chimney openings.

While roost temperature may be an important factor governing differential use of anthropogenic and tree roosts during summer, other factors may also be important. Rafinesque's big-eared bats that use bridges as day roosts in Louisiana select the warmest areas of the bridges even when temperatures are quite high (Ferrara and Leberg 2005a). These areas are also the darkest portions of the bridges where bats are less likely to be detected by terrestrial predators. Although we did not measure light levels in trees and anthropogenic structures, it was often possible to spot bats under bridges and in the building without the aid of a light. It was never possible to see bats in trees without a light source. This suggests that bats were not using anthropogenic structures more often than trees due to light levels and that other features of anthropogenic structures may have reduced the risk of predation. For example, bats that used bridges often roosted in the middle of the bridge over water, putting them out of reach of snakes and raccoons, both of which were observed under bridges.

Although use of anthropogenic structures was not lower in winter than in fall and spring, there was a general trend for use to decline in winter as in tree roosts. We were not able to survey trees with chimney-only openings due to logistical constraints. However, Rice (2009) found that Rafinesque's big-eared bats in Louisiana often moved from trees with basal-only or basal-plus chimney openings to trees with chimney-only openings during winter. Therefore, it is likely that many of the bats that used anthropogenic roosts and trees with basal and basal-plus chimney openings during spring, summer, and fall moved to trees with chimney-only openings in winter. Lower use of roosts in winter may also be due to changes in clustering behavior. In summer, adult males usually roost by themselves, but during winter we have observed males roosting with large colonies as did Rice (2009) in Louisiana. Large aggregations of bats can increase the roost temperature by as much as 7 °C in summer (Willis and Brigham 2007). Thus, bats may form larger aggregations in winter for thermoregulatory reasons, resulting in fewer roosts being used.

There are few data on multiannual use of anthropogenic roosts by Rafinesque's big-eared bats and even fewer data on multiannual use of tree roosts. Based on large guano accumulations in building roosts in North Carolina, Clark (1990) concluded that Rafinesque's big-eared bats had used these roosts for many years. Jones and Sutkus (1975) reported on a big-eared bat colony that used a house roost over a 3-year period. Lewis (1995) predicted that bats will show greater fidelity to rare but stable roosts such as bridges and buildings than to more common and less stable roosts such as trees. Rafinesque's big-eared bats in Mississippi show greater short-term fidelity to anthropogenic roosts than to tree roosts (Trousdale and others 2008), and our data suggest that longer term fidelity to anthropogenic roosts was also greater and more consistent than to tree roosts. All five anthropogenic roosts were used in all 4 years of the study. We also checked these structures prior to and after the study, and all were used for at least 6 years. In contrast, only four of nine tree roosts that were examined throughout the study were used in all 4 years. However, most roost trees we found were used for at least 2 years and many for 3 years. In some cases, multiannual use was by one bat or group of bats, and in some cases it was by a succession of bats.

Multiannual use of crevice and cavity roosts has been found in several other bat species. For example, crevice roosts in ponderosa pine (*P. ponderosa*), alligator juniper (*Juniperus deppeana*), and pinyon (*P. edulis*) in New Mexico were reused by female long-eared myotis (*Myotis evotis*), fringed myotis (*M. thysanodes*), long-legged myotis (*M. volans*), and big brown bats during 75 percent of the summers they were monitored, 1 to 3 years postidentification (Chung-MacCoubrey 2003). In Canada, 6 of 11 big brown bat cavity roosts in live trembling aspen (*Populus tremuloides*) were used in the 2 years following their identification as roosts (Willis and others 2003). Willis and others (2003) also checked some trees that had been identified as roosts during a previous study and found that some of those trees were used 8 to 10 years after they were first identified as roosts. We only observed tree roosts for 4 years, and observations of these trees over longer periods of time will be necessary to fully understand long-term roost use by Rafinesque's big-eared bats. Nonetheless, our observations of multiannual use of anthropogenic and tree roosts suggest that long-term preservation of these roosts may be critical for long-term conservation of these bats, particularly in areas where roosts may be limiting. In addition, six tree roosts fell or broke during the 4 years of this study, suggesting the importance of recruiting new trees into the "roost tree population." We suggest that trees with small cavities also be conserved as many of these are likely to become suitable roost trees in future years.

CONCLUSIONS

Our data suggest that factors affecting use of roosts by Rafinesque's big-eared bats in bottomland hardwood forests may vary with roost type and season. Thus, conclusions based on data from anthropogenic roosts may not apply to tree roosts and vice versa. Our data also suggest that bats responded differently to environmental conditions among seasons and roost types. Because Rafinesque's big-eared bats in the Coastal Plain are typically found in an area throughout the year (this study, Rice 2009, Trousdale and Beckett 2004), studies of these bats should be conducted year round, when possible, to identify environmental and habitat factors affecting these populations. We encourage future studies of microclimate conditions within and between roost types to more fully understand roost selection by Rafinesque's big-eared bats on an annual basis. The long-term use of both anthropogenic and tree roosts by these bats emphasizes the importance of such structures to the ecology of Rafinesque's big-eared bats; when these are identified as used by these bats, we recommend that both types of structures be given long-term protection from disturbance and destruction.

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