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Author(s): Jessica S. Lucas, Susan C. Loeb and Patrick G. R. Jodice

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Roost selection by Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) in a pristine habitat at three spatial scales

JESSICA S. LUCAS^{1,2}, SUSAN C. LOEB^{3,5}, and PATRICK G. R. JODICE⁴

¹*School of Agriculture, Forestry, and Environmental Sciences and U.S. Geological Survey South Carolina Cooperative Fish*

²*Wildlife Research Unit, Clemson University, Clemson, SC 29634, USA*

³*USDA Forest Service, Southern Research Station, Clemson University, Clemson, SC 29634, USA*

⁴*U.S. Geological Survey, South Carolina Cooperative Fish and Wildlife Research Unit, Clemson University, Clemson, SC 29634, USA*

⁵*Corresponding author: E-mail: sloeb@fs.fed.us*

Although several studies have described roost use by Rafinesque's big-eared bats (*Corynorhinus rafinesquii*), few studies have examined roost selection. We examined roost use and selection by Rafinesque's big-eared bat at the tree, stand, and landscape scales during the maternity season in pristine old-growth habitat in the Coastal Plain of South Carolina. We located 43 roosts (14 maternity, 29 solitary) through cavity searches and radio-telemetry. Maternity colonies and solitary individuals selected roosts based on similar characteristics. The best model explaining roost selection by all bats included tree and stand characteristics; landscape factors had little influence on roost use. Bats selected large diameter trees in areas with a high density of trees with cavities in the surrounding area. Most roosts (67.4%) were in water tupelo (*Nyssa aquatica*) in semi-permanently flooded and saturated areas. Half of maternity roost cavities had upper bole openings whereas only 25.8% of solitary roosts had upper bole openings. Bats that roosted with maternity groups stayed in roosts for significantly shorter periods of time (1.3 ± 0.1 days) and used significantly more roost trees (5.0 ± 0.6 roosts) than adult males (3.8 ± 1.10 days, 2.3 ± 0.4 roosts, respectively). Maternity colony use of cavities with upper bole openings and shorter residency times suggest that predator avoidance may have been an important factor governing roosting behavior of maternity colonies in this area. Our results suggest that retention of large diameter, hollow trees in wetland areas will benefit Rafinesque's big-eared bat individuals and maternity colonies in this area.

Key words: bottomland hardwoods, predator avoidance, Rafinesque's big-eared bat, roost selection, roost fidelity

INTRODUCTION

Because bats spend the majority of their time in day roosts, these structures are particularly important in their ecology and evolution (Barclay and Kurta, 2007). Roosts provide relatively stable microclimates that minimize energy expenditures, provide protection from predators, and are sites for social interactions, mating, and raising young (Kunz and Lumsden, 2003). Sex, group size, reproductive status, season, predation risk, parasite load, and microclimate can all influence roost use and selection in bats (Kerth *et al.*, 2001; Veilleux *et al.*, 2004; Ferrara and Leberg, 2005; Reckardt and Kerth, 2007; Willis and Brigham, 2007). Most studies of roost site selection in bats have focused on characteristics of the roost and its surrounding area (Kalcounis-Rueppell *et al.*, 2005). However, factors at larger spatial scales may also influence roost site

selection but have received less attention (Miles *et al.*, 2006; Limpert *et al.*, 2007; Perry *et al.*, 2008). At the microhabitat level, North American bats generally select roost trees that are taller, larger in diameter, and have more open canopies than random trees (Kalcounis-Rueppell *et al.*, 2005). At the macrohabitat scale, forest type and structure are important factors in roost selection (Perry *et al.*, 2007; Webala *et al.*, 2010) whereas at the landscape scale, factors such as distance to water, distance to openings, forest area, and degree of urbanization or development have been shown to be important (Miles *et al.*, 2006; Watrous *et al.*, 2006; Limpert *et al.*, 2007; O'Keefe *et al.*, 2009).

Male and female bats often roost separately, particularly during the breeding season when females form maternity colonies (Hamilton and Barclay, 1994; Kunz and Lumsden, 2003). Reproductive females have different roosting requirements than

those of solitary males and non-reproductive females. Roost selection by reproductive females is related to cavity size (Willis *et al.*, 2006), proximity to foraging areas (Henry *et al.*, 2002), temperature (Kerth *et al.*, 2001), tree size (Perry and Thill, 2007a), and stand composition (Perry and Thill, 2007b). Because temperature influences bat fetal and juvenile growth rates, differences in roost site selection between reproductive females and males and non-reproductive females are often attributed to differences in the thermal properties of roosts (Hamilton and Barclay, 1994; Kerth *et al.*, 2001; Lausen and Barclay, 2006). However, predation risk and parasite loads may also be important factors in roost selection (Ferrara and Leberg, 2005; Ruczyński and Bogdanowicz, 2005; Reckardt and Kerth, 2007; Clement and Castleberry, 2013b) although these hypotheses have received less study.

Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) are found throughout the southeastern United States but are a species of special concern in every state within their range (Bayless *et al.*, 2011). Habitat destruction, particularly roost destruction, is a major factor in the species' putative decline in the Coastal Plains because a large portion of bottomland hardwood forest has been harvested over the past century (Kellison and Young, 1997; Miller *et al.*, 2011). Rafinesque's big-eared bats are non-migratory and use a variety of roost structures including caves (Hurst and Lacki, 1999), man-made structures (e.g., Jones and Suttikus, 1975; Clark, 1990; Lance *et al.*, 2001), and hollow trees (e.g., Carver and Ashley, 2008; Johnson and Lacki, 2011). Within the Coastal Plains, big-eared bats are associated with bottomland hardwood forests for both foraging and roosting (Clark, 1990; Trousdale and Beckett, 2005; Johnson and Lacki, 2013); females form maternity colonies in the spring and summer while males remain solitary for most of the year (Jones, 1977). Like most forest bats, big-eared bats frequently switch roosts (Trousdale and Beckett, 2005; Trousdale *et al.*, 2008; Johnson *et al.*, 2012) but frequency of roost switching and the number of roosts per bat or colony has received little study.

Although several studies have described Rafinesque's big-eared bat roost structures and habitat in the Coastal Plains (e.g., Clark, 1990; Lance *et al.*, 2001; Gooding and Langford, 2004; Mirowsky *et al.*, 2004; Johnson and Lacki, 2011; Roby *et al.*, 2011), only three studies (Carver and Ashley, 2008; Clement and Castleberry, 2013b; Fleming *et al.*, 2013) have examined roost site selection (i.e., use relative to availability) and only Clement and

Castleberry (2013b) examined differences in roost selection between maternity colonies and solitary individuals. Site characteristics and landscape factors affecting roost selection have rarely been addressed (Trousdale, 2011; Fleming *et al.*, 2013). Conservation and recovery of Rafinesque's big-eared bats will be greatly aided by understanding their habitat associations and requirements at various spatial scales. Further, many studies have been conducted in disturbed habitats (e.g., Trousdale and Beckett, 2005; Johnson and Lacki, 2011; Roby *et al.*, 2011). While these studies are very informative, studies in relatively pristine habitats provide reference points for future habitat restoration. Thus, we examined roost use, selection, and fidelity of Rafinesque's big-eared bats during the maternity season (May through August) and tested whether bats selected roosts based on tree, stand, or landscape characteristics in Congaree National Park (CONG), which contains the largest expanse of old-growth bottomland hardwood forest remaining in the U.S. We also tested for differences in roost selection between maternity colonies and solitary individuals. Because CONG most closely represents the pre-colonial landscape, it represents those conditions that most likely influenced the evolution of roosting behavior of this species in the Coastal Plains.

MATERIALS AND METHODS

Study Site

CONG is located about 30 km southeast of Columbia, South Carolina in Richland County (Fig. 1) in the Upper Coastal Plain Physiographic Region. Approximately 80% of the 9,000 ha park is composed of bottomland hardwood forest. Common overstory species in bottomland sites are water tupelo (*Nyssa aquatica*), swamp tupelo (*N. sylvatica biflora*), and bald cypress (*Taxodium distichum*). A variety of mixed upland hardwoods occur throughout the rest of the park including oaks (*Quercus* spp.), sweetgum (*Liquidambar styraciflua*), American beech (*Fagus grandifolia*), Carolina ash (*Fraxinus caroliniana*), and red maple (*Acer rubrum*). The majority of properties bordering CONG have been converted to agriculture or hunting leases. The southern border of the park is marked by the Congaree River and Cedar Creek, a second-order blackwater stream, supports the interior bottomland hardwood forest of the park (Fig. 1). CONG experiences an average of 10 floods per year that cover 75% of the park and 90% of the park is flooded at least once a year. The climate of CONG is hot, humid subtropical. Mean minimum summer (May–August) temperatures from 1971 to 2000 ranged from 16.1°C to 21.9°C and mean maximum temperatures ranged from 29.8°C to 34.3°C (http://www.sercc.com/climateinfo/historical/historical_sc.html). Mean monthly precipitation during May through August ranges from 85.1 mm to 137.2 mm. Research was limited to the

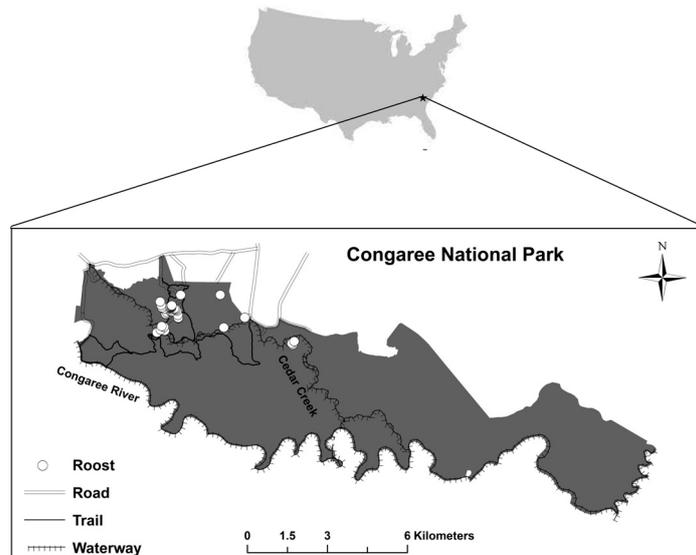


FIG. 1. Location of Congaree National Park within South Carolina and the location of roosts within the park

western third of the park where gravel roads and trails provided access (Fig. 1).

Capture and Telemetry Procedures

The study was conducted from May through August 2006 and 2007. Roosts were located via tree searches and radio telemetry. We opportunistically searched for trees in areas that appeared suitable for big-eared bat roost trees such as cypress-tupelo bottomlands and along streams and sloughs, or in habitat plots surrounding roost and random trees (see habitat section below). All trees with basal cavity openings were examined with a spotlight and mirror for the presence of big-eared bats.

Bats were captured for radio-telemetry in mist nets set in fly-ways or from roosts identified via tree searches. Mist nets were checked every 10 min from dark until at least midnight, depending on weather conditions. We placed mist nets over cavity openings to capture bats upon emergence from cavities with basal openings or used a hand net to capture bats just prior to emergence. Mist nets were set close to trees that contained colonies instead of directly on them to prevent too many bats from being captured at once.

Upon capture, we determined species, weight, sex, reproductive condition, and forearm length of each bat. We categorized males as scrotal or non-scrotal and females as pregnant (by palpation), lactating, post-lactating, or non-reproductive. We aged each bat (juvenile or adult) using a bright light behind the wing, looking for the unfused epiphyses characteristic of juvenile bats (Anthony, 1988). All bats were fitted with a numbered aluminum lipped band on their forearm for identification; Rafinesque's big-eared bats were also fitted with a colored plastic band for aid in verification of radio-tagged bat roost locations. We attached a 0.46 g transmitter (LB-2N, Holohil Systems Limited) to all big-eared bats captured. Transmitters were attached between the scapulae using surgical adhesive and bats were held until the glue dried (approximately 15–30 min). Mean body mass of radio-tagged bats was 8.51 g (range = 6.75–10.25) and transmitters represented 4.5–6.8% of body

mass. Although it has been suggested that a transmitter should not be > 5% of a bat's body mass (Aldridge and Brigham, 1988), generally this 'rule' is aimed towards foraging studies. For this study on roosting, we expected that a slight increase over 5% would not change roosting behavior. Procedures used in this study were approved by the Clemson University Animal Use and Care Committee (06-ARC-030).

We tracked each bat to its roost the day after capture and each successive day for the life of the transmitter or until the transmitter detached, using a receiver (TRX-2000S, Wildlife Materials International, Inc.) and 3-element Yagi antenna. When possible, we verified that the bat was in the tree by looking inside the cavity with a spotlight and mirror and counted or estimated the number of bats present in the roost with the radio-tagged bat. If visual inspection of the roost was not possible, we watched potential roost exits from just before sunset until it was too dark to identify bats, and recorded all exiting bats and their location.

Roost Tree and Habitat Measurements

For each roost tree, we recorded characteristics that were thought to be important for roosting big-eared bats based on previous studies (Trousdale, 2011) including cavity opening position (basal or upper bole), cavity opening dimensions, number of openings, cavity opening orientation, roost tree canopy position (midstory or overstory), tree height, decomposition state (Thomas *et al.*, 1979), diameter at breast height (dbh), and species. A decomposition state of 1 indicated a live healthy tree, 2 a live damaged tree, 3 a new snag with most of its branches and bark, and 4–9 various states of snag decay with 9 representing a stump. Internal cavity dimensions were recorded if possible. Internal width was measured with a tape whereas height was estimated with the aid of a clinometer. Each roost was marked with a numbered aluminum tag and mapped using a Garmin GPSMAP 76CS. We also recorded these variables for each tree ≥ 10 cm dbh within a 17.8 m radius circular plot (0.1 ha) around each roost tree. All accessible cavities within the plot were checked for bats.

We located comparison trees within CONG to test whether big-eared bats selected roost trees based on tree, plot, or landscape characteristics. We used a grid established by park staff to conduct searches for the ivory-billed woodpecker (*Campephilus principalis*) and selected grid cells that contained known big-eared bat roost trees. Cells in this grid varied in size (120–240 ha) and were generally based on natural landmarks for delineation. The selected grid cells were overlaid on The Nature Conservancy (TNC) GIS vegetation layer derived from 1996 USGS aerial photography (1 : 12,000) in ARCGIS Version 9.1 (Environmental Systems Research Institute, Inc., Redlands, CA). Because the majority of roost trees (76.7%) were in cypress-tupelo-ash stands, we generated random points within these stand types using AlaskaPak (National Park Service software). Points that fell in major water bodies were omitted and new points were generated using the original selection criteria for random points. The comparison or random tree was defined as the closest tree >35 cm dbh to the random point. We used this minimum tree size as it represented the dbh of the smallest roost tree. Many roosts were in trees with openings in the upper bole and these openings were not always apparent from the ground until we saw the bats emerge from them. Thus, we did not restrict our selection of random trees to only those with obvious cavities. We recorded the same data for each random tree as were collected for roost trees. We also measured all trees in the 0.1 ha plot surrounding the original point. If a big-eared bat was found in a cavity in the random plot, it became the center of a roost tree plot and two new random plot centers were generated.

We created a point layer of the roost tree coordinates in ArcGIS Version 10.0 and overlaid this layer on the TNC vegetation layer to determine general habitat associations of roost locations. Although this layer was approximately 10 years old, there is no active management in CONG and no major disturbances such as hurricanes or tornados had occurred in the previous 10 years. We also overlaid the roost tree layer on the U.S. Fish and Wildlife Service National Wetland Inventory database (<http://www.fws.gov/wetlands/>) to determine the wetland type of each roost tree location.

The distance to nearest habitat edge (change in habitat type defined by the TNC vegetation layer) was calculated using the ‘Near’ tool in ArcMap Version 9.1. Distance to nearest permanent water features was measured from the tree to the nearest creek, lake, or pond. Although distance to ephemeral water sources could be important, selection of these resources for use in an analysis would be largely subjective. In addition, most of the park is subject to flooding during significant rain events and would be within a short distance of some ephemeral water source at any given date.

Statistical Analysis

Although solitary individuals observed in roost trees were most likely males, we were not able to verify this in all cases. Thus, we use the term ‘solitary individuals’ except when data were based on known individuals (i.e., from radio-tagged individuals). Roosts used by both solitary individuals and maternity colonies were considered maternity colonies in the analyses to assure independence in the data analyses. We used Moran’s I in ArcGIS 9.1 to test whether roost and random trees were clustered or randomly distributed.

To examine roost switching, we only used data for bats tracked for at least four days. For days that we searched for, but

could not locate a bat, we assumed that the bat was in an unknown roost if we located it again later. Days on which we did not track the bat were not used in the calculations. We calculated roost switching by dividing the total number of days that each bat was located by the number of roost changes of the bat during the tracking period (Kurta *et al.*, 2002). We used *t*-tests to test for differences in roost fidelity between solitary individuals and the adult female/juveniles. Means \pm 1 SE are reported.

We used a principal components analysis (PCA; R v. 2.8.1, package ‘Vegan’) to test whether tree species composition in plots surrounding roost and random trees differed. One roost tree was removed from the analysis because it was an extreme outlier and it dominated axes of the PCA analysis. The first three PCA axes were tested for significance using MANOVA (0.05 significance level). Each axis was then individually tested using ANOVA, to determine if roost and random plots differed by axis. A Wilcoxon test was conducted in the event of non-normality of data. We interpreted the PCA loadings to define tree species that are important in big-eared bat roost selection.

We used a two-step process to model roost selection of big-eared bats in CONG. First we ran a set of logistic regression models to test for differences in roost use by maternity colonies and solitary individuals. We then ran a second set of models to compare all roost trees to random trees. We developed a priori logistic regression models at the tree, stand, and landscape scales, and all combinations of the three scales (Table 1). We ran all 8 models (including the Null model) for both sets of models using SAS 9.3. We ran a correlation analysis to determine that no variables were highly correlated ($r > 0.70$) and tested the fit of the model using the Hosmer-Lemeshow test on the global models. Both sets of models were an adequate fit ($\chi^2_8 = 4.93$, $P = 0.76$ and $\chi^2_8 = 3.39$, $P = 0.91$ for solitary versus maternity colony roosts and all roosts versus random trees, respectively). We used an information theoretic approach to select models and used Akaike’s Information Criterion corrected for small sample sizes (AIC_c). We calculated the model averaged parameter estimates and unconditional standard errors for the model set that made up > 90% of the model weights (Burnham and Anderson, 2002). Model parameters with 95% confidence intervals that did not include 0 were considered significant. Because we could not measure cavity dimensions (opening size, internal dimensions, aspect) on cavities with upper bole openings, these variables were not included in the models.

RESULTS

We captured 15 Rafinesque’s big-eared bats, 12 southeastern myotis (*Myotis austroriparius*), eight tri-colored bats (*Perimyotis subflavus*), two evening bats (*Nycticeius humeralis*), two big brown bats (*Eptesicus fuscus*), and five red bats (*Lasiurus borealis*). Fourteen of the 15 big-eared bats captured were males and one was female. At the time of capture, 13 males were non-scrotal, one male was scrotal, and the female was lactating. All big-eared bats were adult with the exception of two juvenile males. All 15 big-eared bats were radio-tagged and we were able to obtain roost data from 13 of them.

TABLE 1. Variables included in the three spatial scale models of *C. rafinesquii* roost selection. Note: Cavity location was only used in models that tested differences between males and females and Wetland Type was only used in models that tested differences between roosts and random trees

| Model | Variables | Definition |
|-----------|-------------------|---|
| Tree | Species | <i>Nyssa aquatica</i> (1) or other (0) |
| | Dbh | Roost or random tree diameter at breast height (cm) |
| | Height | Roost or random tree height (m) |
| | Cavity location | Basal or upper bole opening |
| Stand | Basal area | Total basal area of surrounding the roost or random tree (m ² /0.1 ha) |
| | Density | Density of trees surrounding the roost or random tree (trees/0.1 ha) |
| | Stand composition | PCA scores of first two significant axes |
| | Percent cavities | Percent of trees within 0.1 ha that had potential roost cavities |
| Landscape | Distance to water | Distance (m) from the roost or random tree to the closest permanent water source |
| | Distance to edge | Distance (m) from the roost or random tree to the nearest change in habitat type as defined by the TNC vegetation layer |
| | Habitat type | <i>Cypress-tupelo</i> (1) or other (0) |
| | Wetland type | Seasonally flooded, semi-seasonally flooded or saturated, and temporally flooded or upland |
| | | |

We located 43 roosts (12 maternity, 29 solitary and two that were used by both groups) from radio-tagged big-eared bats and tree searches. Radio-tagged males always roosted singly. Visual confirmation was made for all roosts. Of the 43 roost trees identified, 32 were located with telemetry (74.4% of all roosts) and 11 (25.6%) were found via tree searches. The maternity roosts were located by tracking the lactating female as well as the two juvenile males who were still roosting with maternity colonies.

Radio-tagged bats were tracked for an average of 9.1 ± 2.9 days (range 1–14); the adult female and juvenile males were tracked for an average of 9.0 ± 2.1 days and adult males were tracked for an average of 9.1 ± 1.5 days. Mean number of roosts per individual was 3.1 ± 0.5 (range 1–6). The average number of roosts used by the juveniles and adult female (5.0 ± 0.6 , $n = 3$, range 4–6) was significantly higher ($t_{3,68} = 3.99$, $P < 0.05$) than the average number of roosts used by adult males (2.3 ± 0.4 ,

$n = 7$, range 1–4). The average number of days per roost for adult males (3.8 ± 1.1 , range 1.2–10) was higher ($t_{6,0} = 2.25$, $P = 0.065$) than the average number of days per roost for the adult female and juveniles (1.3 ± 0.10 , range 1.2–1.4). The average distance among roosts used by juvenile males and the adult female was $187.1 \text{ m} \pm 45.5$ (range 117.0–272.5 m), and the average distance among male roosts was $1032.0 \text{ m} \pm 325.6$ (range 124.5–1896.0 m). Based on exit counts and counts of visible bats within roosts, maternity groups ranged in size from six to approximately 100 individuals, but were typically around 40 individuals. Colony groups varied in size from day to day as bats moved from roost to roost.

Roosts were in large hollows of a few tree species (Table 2). Most solitary (65.5%) and maternity roosts (71.4%) were in water tupelo. Roosts were also in swamp tupelo, baldcypress, sweetgum, *Nyssa* spp., and a snag that could not be identified to species due to decomposition (Table 2). Fifteen of the roosts were in upper bole cavities and 28 were

TABLE 2. Number (and percent) of Rafinesque's big-eared bat roost trees of each species used by maternity colonies and solitary individuals, number (and percent) of random trees of each species, and percent of each species in roost and random plots in Congaree National Park, South Carolina, May–August 2006–2007

| Tree species | Maternity | Solitary | Random trees | Roost plots | Random plots |
|--------------------------------|-----------|-----------|--------------|-------------|--------------|
| <i>Nyssa aquatica</i> | 10 (71.4) | 19 (65.5) | 8 (18.6) | 49.7 | 20.1 |
| <i>Nyssa sylvatica biflora</i> | 3 (25.0) | 3 (10.3) | 14 (32.6) | 7.9 | 19.0 |
| <i>Taxodium distichum</i> | – | 1 (3.4) | 5 (11.6) | 11.1 | 4.9 |
| <i>Liquidambar styraciflua</i> | – | 1 (3.4) | – | 2.2 | 8.1 |
| <i>Nyssa</i> spp. | 1 (8.3) | 4 (13.8) | 1 (2.3) | 2.0 | 3.5 |
| <i>Quercus</i> spp. | – | – | 8 (18.6) | 2.6 | 8.2 |
| Other | – | 1 (3.4) | 7 (16.3) | 24.4 | 36.2 |
| Total | 14 | 29 | 43 | – | – |

in cavities with basal openings. Half (7) of the maternity roosts were in upper bole cavities, whereas only 25.8% of solitary roosts were in upper bole cavities. Mean decomposition state of roost trees was 2.55; 83.7% of roost trees were live-damaged (decomposition state 2) whereas the remainder were dead and in various states of decomposition. Most (76.7%) roost trees were within the baldcypress-water tupelo-Carolina ash vegetation class, which comprised 12.2% of the surrounding area. Roost trees were also located within a sweetgum complex (7.0%), a hackberry complex (11.6%), a beech complex (2.3%), and a tupelo complex (2.3%). The majority of roosts were in semi-permanently (51.2%) and seasonally (32.6%) flooded habitat with few roosts in saturated (2.3%), temporarily flooded (7.0%), or upland (7.0%) habitats. Roost trees were significantly clustered on the landscape (Moran's $I = 4.28$, $P < 0.001$ — Fig. 1) whereas random trees were not (Moran's $I = 1.39$, $P > 0.05$).

Roost and random plots differed significantly in species composition ($F_{2, 82} = 15.61$, $P < 0.001$ — Fig. 2) based on the first three axes. The first two axes were retained for the PCA analysis (eigenvalue = 3.99 for PCA1 and eigenvalue = 2.64 for PCA2). A post hoc ANOVA indicated significant differences between roost and random plots along the first two axes (PC1: $F_{2, 82} = 31.66$, $P < 0.001$; PC2: $F_{2, 82} = 9.07$, $P < 0.05$).

The first PCA axis described 21.9% of the variance in tree species composition; tree species positively associated with roost plots were water tupelo, baldcypress, unidentified decomposed trees, ash, and decomposed *Nyssa* species. Species negatively associated with roost plots were swamp tupelo, sweetgum, American holly (*Ilex opaca*), laurel oak (*Q. laurifolia*), tulip poplar (*Liriodendron tulipifera*), red maple, sweetbay (*Magnolia virginiana*), and water elm (*Planera aquatica*). The second PCA

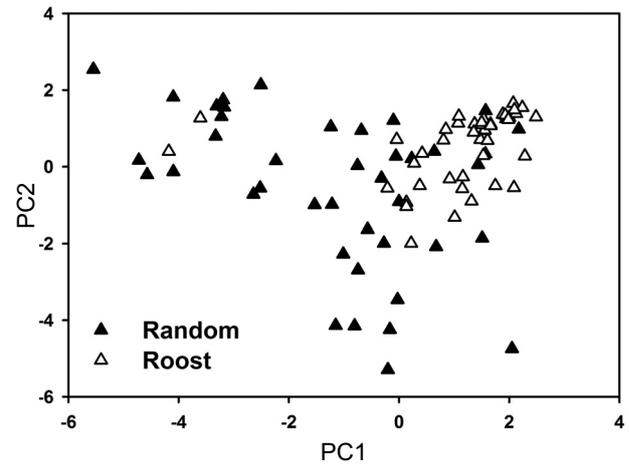


FIG. 2. Plot of first two PCA axes of roost and random tree vegetation plots within Congaree National Park, South Carolina during May–August, 2006 and May–August 2007

axis described 10.4% of the variation in tree species composition; species positively associated with roost plots along this axis were water tupelo and decomposed *Nyssa* species. Other species associated with roost plots included sweetgum, American holly, tulip poplar, and swamp tupelo. Species negatively associated roost plots included American elm (*Ulmus americana*), water elm, unidentified decomposed trees, laurel oak, red maple, ash species, and sugarberry.

The best model explaining differences in roost site selection between maternity and solitary roosts was the Null model (Table 3). The Null model was > three times more likely to be the best model suggesting that there was little difference in roost site selection between maternity colonies and solitary individuals based on the variables included in our models. Although the Tree and Landscape models also had some support (Table 3), all of the parameter estimates had confidence intervals that included 0 (Table 4).

TABLE 3. Number of parameters included in logistic regression models (K), values of Akaike Information Criterion modified for small samples (AIC_c), difference from AIC_{min} (ΔAIC_c), and model weights (ω_i) for top-ranked models that explained differences between male and female *C. rafinesquii* roosts and all roosts versus random trees in Congaree National Park, May–August 2006–2007. Note: Cavity location was only used in models that tested differences between males and females, and wetland type was only used in models that tested differences between roosts and random trees

| Model | K | AIC_c | ΔAIC_c | ω_i |
|--------------------------|----|---------|----------------|------------|
| Male versus female | | | | |
| Null | 2 | 54.280 | 0 | 0.605 |
| Tree | 6 | 56.751 | 2.471 | 0.176 |
| Landscape | 5 | 56.938 | 2.658 | 0.160 |
| All roosts versus random | | | | |
| Tree+Stand | 10 | 69.054 | 0 | 0.829 |
| Tree | 5 | 72.944 | 3.889 | 0.119 |

TABLE 4. Coefficient estimates, standard errors (SE), 95% confidence intervals (CI) on the coefficients and odds ratios for model averaged logistic regression models

| Scale | Variable | Estimate | SE | 95% CI | Odds ratio |
|--------------------------|--------------------------------------|----------|-------|--------------|------------|
| Male versus female | | | | | |
| Tree | Species | -1.305 | 0.969 | -3.204–0.594 | 0.271 |
| | Dbh (cm) | 0.009 | 0.014 | -0.018–0.036 | 1.010 |
| | Height (m) | 0.125 | 0.064 | -0.008–0.250 | 1.133 |
| | Cavity location | 0.885 | 0.765 | -0.674–2.444 | 2.422 |
| Landscape | Distance to water (m) | 0.002 | 0.002 | -0.002–0.005 | 1.002 |
| | Distance to edge (m) | 0.014 | 0.009 | -0.005–0.032 | 1.014 |
| | Habitat type | 0.500 | 0.824 | -1.115–2.114 | 0.544 |
| All roosts versus random | | | | | |
| Tree | Species | 0.891 | 1.026 | -1.120–2.902 | 2.438 |
| | dbh (cm) | 0.042 | 0.014 | 0.015–0.070 | 1.043 |
| | Height (m) | -0.076 | 0.056 | -0.186–0.034 | 0.927 |
| Stand | Plot basal area (m ² /ha) | 0.133 | 0.116 | -0.006–0.360 | 1.142 |
| | % Trees with cavities | 0.261 | 0.118 | 0.030–0.491 | 0.027 |
| | Tree density (no./ha) | 0.029 | 0.026 | -0.023–0.081 | 0.272 |
| | PCA axis 1 | 0.427 | 0.264 | -0.091–0.946 | 0.106 |
| | PCA axis 2 | 0.221 | 0.261 | -0.296–0.733 | 0.398 |

The Tree+Stand model was seven times as likely to be the best model differentiating all roost and random sites, although the Tree model also had some support (Table 3). Diameter at breast height (dbh) and percent of trees with cavities within 0.10 ha were the only variables with parameter estimate confidence intervals that did not include 0 (Table 4). Trees used by big-eared bats were 1.67 times greater in diameter and were surrounded by almost twice as many trees with cavities than random trees (Table 5).

DISCUSSION

Because bats have the ability to move across large distances, landscape features as well as site and stand characteristics are important to consider when developing conservation and management strategies (Duchamp *et al.*, 2007). Landscape features such as amount of forest and urban land in the surrounding area, distance to openings, and distance

to water have been found to affect bat roost site selection (Miles *et al.*, 2006; Watrous *et al.*, 2006; Limpert *et al.*, 2007; O'Keefe *et al.*, 2009). However, the importance of landscape features may vary among sites. For example, Miles *et al.* (2006) found that evening bats (*Nycticeius humeralis*) in natural areas select roosts based on tree, stand, and landscape characteristics whereas in managed landscapes, evening bats select roosts based on tree and stand characteristics only. They hypothesized that the greater number of available roosts in the natural areas allowed bats to select roosts that minimized such things as commuting costs whereas in the managed areas bats had to base selection on the availability of suitable trees wherever they were on the landscape. Despite the pristine nature of CONG, landscape factors had little influence on roost selection by big-eared bats in our study as models that included landscape variables had little support. Instead the most important variables associated with

TABLE 5. Mean and SE of roost characteristics used by *C. rafinesquii* maternity colonies, solitary individuals, all roosts combined and random trees in Congaree National Park, May–August 2006–2007

| Roost characteristic | Maternity colonies | | Solitary individuals | | All roosts | | Random trees | |
|---------------------------------|--------------------|------|----------------------|------|------------|------|--------------|------|
| | \bar{x} | SE | \bar{x} | SE | \bar{x} | SE | \bar{x} | SE |
| Dbh (cm) | 118.8 | 6.6 | 101.2 | 5.9 | 107.1 | 4.7 | 64.1 | 4.2 |
| Height (m) | 30.8 | 1.7 | 25.0 | 1.7 | 26.9 | 1.3 | 25.6 | 1.7 |
| Basal area (m ² /ha) | 130.0 | 6.7 | 115.9 | 6.6 | 120.5 | 4.5 | 71.3 | 5.6 |
| Density (trees/ha) | 501.4 | 41.9 | 518.6 | 31.2 | 513.0 | 24.8 | 523.0 | 19.0 |
| % Trees with cavities | 6.3 | 1.0 | 5.8 | 0.6 | 6.0 | 0.5 | 3.1 | 0.4 |
| Distance to habitat edge (m) | 72.5 | 12.2 | 52.0 | 76.5 | 59.2 | 6.0 | 43.1 | 6.8 |
| Distance to water (m) | 398.1 | 59.4 | 369.3 | 55.5 | 378.7 | 41.8 | 493.2 | 55.7 |

roost selection by big-eared bats were associated with tree and stand level characteristics, specifically dbh and % of trees in the surrounding area with cavities. PCA results also suggested an influence at the stand level.

The lack of a landscape effect may have been due to the fact that most of CONG is mature unmanaged habitat with few hard edges and is relatively homogenous. Further, we found no relationship between roost use and distance to water, similar to findings for Rafinesque's big-eared bats in Georgia and Mississippi (Clement and Castleberry, 2013a; Fleming *et al.*, 2013). The lack of a relationship between big-eared bats and proximity to permanent water in CONG may have been due to few permanent water sources within the park and the abundance of seasonal water sources (sloughs, seasonal channels, ephemeral wetlands) in the areas that bats used. These seasonal and temporary water sources are not apparent in the GIS layers and are difficult to measure. Although wetland type was not a significant variable in our models, we found that the majority of roosts were in semi-permanently flooded areas followed by seasonally flooded areas. Few roosts were in saturated, temporarily flooded, or upland sites. Similarly, in Georgia big-eared bats are twice as likely to use semi-permanently flooded areas as seasonally flooded sites but 20 times as likely to use semi-permanently flooded areas as saturated areas (Clement and Castleberry, 2013a).

Rafinesque's big-eared bats in CONG selected large diameter trees which were similar to those used by Rafinesque's big-eared bats throughout the range (Trousdale, 2011). Reproductive females often select larger diameter and taller trees in areas that receive greater solar radiation than those selected by adult males and non-reproductive females presumably to offset energetic costs associated with gestation and lactation (Hamilton and Barclay, 1994; Lausen and Barclay, 2006). However, roosts used by maternity colonies and solitary individuals in CONG were very similar suggesting that thermoregulatory demands may not have been an important influence on Rafinesque's big-eared bat roost selection in CONG. Rafinesque's big-eared bat maternity colonies and adult males in southern Georgia also select roosts with similar characteristics (Clement and Castleberry, 2013b). The warm temperatures in the southeastern Coastal Plains, even at night, may preclude the need to select roosts based primarily on microclimate, and thermoregulatory concerns may play a much smaller role in roost site

selection than in cooler climates. Selection of large diameter trees may be related to large cavity volume which is an important variable in roost site selection by Rafinesque's big-eared bats in Georgia (Clement and Castleberry, 2013b).

Although maternity colony and solitary roosts did not differ, there were significant differences in several factors related to roosting behavior between the groups including number of roosts used and residency. Further, maternity colonies tended to use cavities with upper bole openings more than solitary individuals. These differences between maternity colonies and solitary individuals suggest that predation may be affecting roosting behavior of Rafinesque's big-eared bat maternity colonies in CONG. Maternity colonies are more vulnerable to predators than solitary individuals because non-volant young cannot use evasive flight if a predator enters the cavity (Gellman and Zielinski, 1996; Clement and Castleberry, 2013b), and the large number of animals in a maternity colony may attract predators due to increased scent, noise, or visibility. Thus, maternity colonies should select roosts that are less vulnerable to predators than solitary roosting individuals or exhibit behaviors that reduce the risk of predation. The use of cavities with upper bole openings may reduce predation risk because it may be more difficult for predators to access upper bole cavities compared to basal cavities (Vanhof and Barclay, 1996; Ruczyński and Bogdanowicz, 2005). However, cavities with upper bole openings may also be used because they provide protection in the case of rapidly rising water (Hofmann *et al.*, 1999), a regular event in floodplain habitats such as CONG.

Maternity colonies also switched roosts more often and used a greater number of roosts than adult males. Predators may be attracted to roosts with a large number of individuals due to increased noise or scent associated with large aggregations and switching roosts frequently may prevent predators from keying in on a particular roost (Barclay *et al.*, 1982; Fenton *et al.*, 1994; Ruczyński and Bogdanowicz, 2005). However, roost fidelity does not differ between males and females in all Rafinesque's big-eared bat populations (Trousdale *et al.*, 2008; Johnson *et al.*, 2012). In Mississippi, where natural roosts are scarce, adult male and female Rafinesque's big-eared bats do not differ in their roost fidelity or the number of roosts used (Trousdale *et al.*, 2008). Bats in that study area use many artificial roosts which may result in high fidelity by all groups. Maternity colonies in CONG may have also

switched roosts more often due to greater parasite loads that built up due to a greater number of individuals. However, ectoparasite loads had little influence on movements of big brown bats among roost sites in Colorado (Ellison *et al.*, 2007).

Bat roosts were clustered on the landscape and bats selected roosts that were surrounded by a higher proportion of trees with cavities. The availability of a high number of cavities in the surrounding area may make potential roosts more attractive due to the accessibility of alternate roosts. Selecting a roost tree within a small area that also provides additional suitable roosts may facilitate movement to alternate roosts if bats are disturbed or a roost is lost, and may reduce energetic costs of switching roosts and predation risks, particularly for maternity colonies when the young are non-volant or newly volant. For example, Rafinesque's big-eared bat females with attached young fly slowly and with difficulty, and can be easily captured by hand while in flight (Jones and Suttkus, 1971).

The majority of trees used by Rafinesque's big-eared bats were water tupelo which appears to be an important roost tree in many areas of the species range (Gooding and Langford, 2004; Trousdale and Beckett, 2005; Carver and Ashley, 2008), possibly due to the species' tendency to develop heart rot and form hollows (Burns and Honkala, 1990). However, in some areas, species such as bald cypress are selected (Johnson *et al.*, 2012), and selection of roost tree species may depend on availability, access, and tree characteristics (Trousdale, 2011).

Our results suggest that in large tracts of old-growth bottomland hardwood forests, Rafinesque's big-eared bats select roosts based on tree and stand characteristics, particularly dbh and the availability of alternate cavities in the surrounding area. Our data demonstrate that conservation of large, hollow water tupelos will benefit Rafinesque's big-eared bat individuals and maternity colonies in this area. Further, because roosts are clustered on the landscape and maternity colonies switch roosts more often and use more roosts than adult males, clusters of roost trees and potential roost trees will provide higher quality habitat compared to individual or isolated trees.

The large extent of old-growth bottomland hardwood forest in CONG likely represents those conditions that are closest to pre-colonial conditions. However, roost selection may vary considerably within species based on roost availability. For example, the diversity of roost types used by long-eared myotis (*Myotis evotis*) increases as the availability

of snags on the landscape decreases (Arnett and Hayes, 2009) and niche breadth of roost sites of *Nyctalus noctula* and *N. leiseri* increase in managed areas compared to more pristine habitats (Ruczyński *et al.*, 2010). In areas where natural roosts are lacking Rafinesque's big-eared bats are more likely to use a variety of artificial roosts (Trousdale *et al.*, 2008). Thus, roost use and selection by Rafinesque's big-eared bats in more disturbed areas than CONG may differ from what we observed. However, our results can serve as a benchmark for restoration of these more disturbed sites.

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