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Adaptive response to land-use history and roost selection by Rafinesque's big-eared bats

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Although habitat loss and degradation are major contributors to species declines, some species are able to adapt to changes in land use by selecting different habitats or structures in disturbed areas than they do in more pristine habitats. Bats are particularly vulnerable to changes in land use due to their dependence on specific habitat types and structures. The objective of this study was to determine how selection and use of roost trees, and niche breadth of Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) varied with land-use history. I examined use and selection of roosts at 3 bottomland hardwood sites that varied in amount and time since timber harvest. Forty-nine transects were established as a means of searching for bats in trees with basal cavity openings and were surveyed 2–9 times. Bats at the most-disturbed sites exhibited the broadest niches, using a greater number of tree species and habitat types, although bats at the least-disturbed site used a broader range of cavity volumes. Cavity characteristics were the primary factors governing roost selection by Rafinesque's big-eared bats, but selection varied among sites. Probability of use increased with increasing cavity volume for bats at all sites, but bats at the most-disturbed site primarily used trees in the smallest cavity volume class, whereas bats at the least-disturbed site primarily used trees in the largest cavity volume class. Results of this study suggest that Rafinesque's big-eared bats can adapt to a range of habitat conditions if trees with large cavities are available. However, future studies need to determine the long-term viability of this species in disturbed habitats.

Key words: adaptive response, *Corynorhinus rafinesquii*, detection probability, land-use history, occupancy, Rafinesque's big-eared bats, roost selection

Habitat loss and degradation are major contributors to species declines worldwide (e.g., Wilcove et al. 1998; Martinuzzi et al. 2015). Highly specialized species are particularly vulnerable to habitat loss and often show significant population declines in response to changes in land use (e.g., Harcourt et al. 2002; Safi and Kerth 2004). However, some species are able to adapt to changes in land use by selecting different habitats or structures in disturbed sites than they do in more pristine areas (Ruczyński et al. 2010; Browne and Paszkowski 2014; Knopff et al. 2014; Toth et al. 2015). For example, habitat selection by western toads (*Anaxyrus boreas*) varies with land-cover type in northern Canada (Browne and Paszkowski 2014), and cougars (*Puma concolor*) in more rural areas avoid anthropogenic structures to a much greater degree than those in more developed areas (Knopff et al. 2014). Because land-use patterns affect the availability of many resources, understanding species responses to variation in habitat quality based on land-use history is critical for designing appropriate area-specific management strategies (Lacki et al. 2010).

Bats are particularly vulnerable to changes in land use because of their dependence on specific habitat types and structures (Voight and Kingston 2015). Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) is a small insectivorous bat found throughout the southeastern United States, from Texas in the west to Florida in the east, and as far north as southern Illinois (Bayless et al. 2011). They are considered rare throughout their range and are presumed to have been extirpated in Ohio and Indiana. Several factors may be contributing to rarity and local extirpation of this species. Rafinesque's big-eared bats have broad, short, rounded wings which allow them to glean insects from vegetation and other surfaces, but also increase their risk of extinction due to higher flight costs and limited abilities to disperse over large distances (Safi and Kerth 2004). In the northern portion of their range, they roost in a variety of roosts including caves, rock shelters, artificial roosts, and tree cavities (Johnson and Lacki 2014) but in Coastal Plain regions, they are closely associated with mature bottomland hardwood

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forests (Bat Conservation International and Southeastern Bat Diversity Network 2013). These forests experienced significant declines (~80%) during the 18th, 19th, and early 20th centuries due to conversion to agriculture (Wear and Greis 2002). Although losses stabilized in the latter part of the 20th century, 256,300 ha (1.2% of total acreage) of bottomland hardwood forests were lost between 2004 and 2009 primarily due to urban and rural development and timber harvest (Dahl 2011). Loss of bottomland hardwood forests is considered 1 of the most significant threats to the long-term viability of this species (Bat Conservation International and Southeastern Bat Diversity Network 2013).

Within bottomland hardwood forests, Rafinesque's big-eared bats usually roost in cavities in large hollow trees (Trousdale 2011). They also use a variety of artificial roosts such as bridges (Lance et al. 2001; Trousdale and Beckett 2004; Bennett et al. 2008), old houses and barns (Clark 1990), and abandoned wells (Sasse et al. 2011). Roost use and selection appears to vary across sites. For example, in western Kentucky, bald cypress (*Taxodium distichum*) is the most commonly used tree (70.3%) for roosting (Johnson and Lacki 2013), whereas tupelo (*Nyssa* spp.) are the most commonly used roost trees in western Tennessee, Georgia, Louisiana, and South Carolina (> 86.5%—Gooding and Langford 2004; Carver and Ashley 2008; Clement and Castleberry 2013; Lucas et al. 2015). In some sites, no particular species of tree is the dominant roost tree, and bats use a wide variety of tree species including oaks (*Quercus*), eastern cottonwood (*Populus deltoides*), American sycamore (*Plantanus occidentalis*), and *Magnolia* spp. (Trousdale and Beckett 2005; Fleming et al. 2013a). In general, Rafinesque's big-eared bats select roosts that are larger in diameter and have larger cavity volumes than randomly selected trees (Clement and Castleberry 2013; Fleming et al. 2013a; Lucas et al. 2015). However, there is considerable variation in sizes of trees used by Rafinesque's big-eared bats across study sites, with mean diameters ranging from 79 to 155 cm, almost a 100% difference (Trousdale 2011). The cause of variation in roost use is not known, but variation in roost fidelity and network structure by Rafinesque's big-eared bats was attributed to variation in roost availability (Trousdale et al. 2008; Johnson et al. 2012). The effects of roost availability and management history on use and selection of roosts have not been examined in Rafinesque's big-eared bats, but have been shown to be of value in other species (Miles et al. 2006; Ruczyński et al. 2010; Russo et al. 2010; Borkin et al. 2011).

In 2013, a conservation strategy was developed for Rafinesque's big-eared bats and southeastern myotis (*Myotis austroriparius*—Bat Conservation International and Southeastern Bat Diversity Network 2013). The strategy outlines many conservation actions that need to be implemented, including identifying occupied habitat, managing habitat around roost trees (e.g., maintaining clear access to openings), identifying and creating new roosting sites, and managing foraging habitat. Developing effective plans that include these actions will rely on greater understanding of the factors that affect use and selection of roost sites and better models to predict presence of big-eared bats in an area. Recent studies suggest that landscape features such as distance to water, distance to roads, and distance to forest edge have little effect on roost selection by Rafinesque's big-eared bats (Clement and Castleberry 2013; Fleming et al. 2013a; Lucas et al. 2015). This suggests that concentrating on roost and habitat features (e.g., forest structure and composition, hydrological conditions) may be the best approach for developing conservation and restoration plans.

My objective was to investigate how tree and stand characteristics affect use and selection of roost trees by Rafinesque's big-eared bats and test whether these characteristics vary with land-use history. I examined use and selection of roosts at 3 sites that varied in the amount and time since timber harvest in bottomland habitats and surrounding areas. I hypothesized that roost selection would vary by site, and that Rafinesque's big-eared bats in more-disturbed sites would expand their roost niche and use a greater diversity of tree species, habitat types, and roost structures than those in less-disturbed sites.

Materials and Methods

Study areas.—The 3 study sites were the Department of Energy, Savannah River Site (SRS, 33°12′38″N, 81°35′26″W) in Aiken and Barnwell Counties, South Carolina; Groton Plantation (GP, 32°45′12″, 81°22′61″) in Allendale and Hampton Counties, South Carolina; and the James W. Webb Wildlife Center and Management Area (Webb, 32°35′36″, 81°18′19″) in Hampton County, South Carolina. All 3 sites are in the Savannah River Floodplain (Fig. 1).

SRS is an 80,267-ha National Environmental Research Park site located in the Upper Coastal Plain and Sandhills Physiographic regions. SRS primarily contains upland pine and hardwood forest with approximately 20% of the site consisting of stream swamp, river swamp, bottomland hardwood, and blackwater stream bottom forests (Imm and McLeod 2005). The Savannah River runs along a 30-km stretch of the site. The swamp is 3–4 km wide and was formed behind a 6- to 10-m high natural levee. Throughout the swamp there are scattered upland ridges that were formed by previous levees that were left when the river channel shifted (Sharitz et al. 1974). Common bottomland species are bald cypress, water tupelo (*N. aquatica*), swamp tupelo (*N. biflora*), sweetgum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), green ash (*Fraxinus pennsylvanica*), willow oak (*Q. phellos*), and laurel oak (*Q. laurifolia*—Imm and McLeod 2005). SRS has a long history of logging for a variety of uses but primarily for agriculture (White 2005). However, little disturbance occurred in the bottomlands until the early 1900s when extensive logging of cypress along the swamp and several of the streams occurred. Further disturbance to bottomland hardwood forests occurred along 3 of the major streams that drained into the swamp during 1960s–1980s when hot-water effluent from nuclear production facilities impacted much of the forest canopy (Sharitz et al. 1974). High-grade logging also occurred in the northern section of the swamp area (the Crackerneck area) during the 1990s.

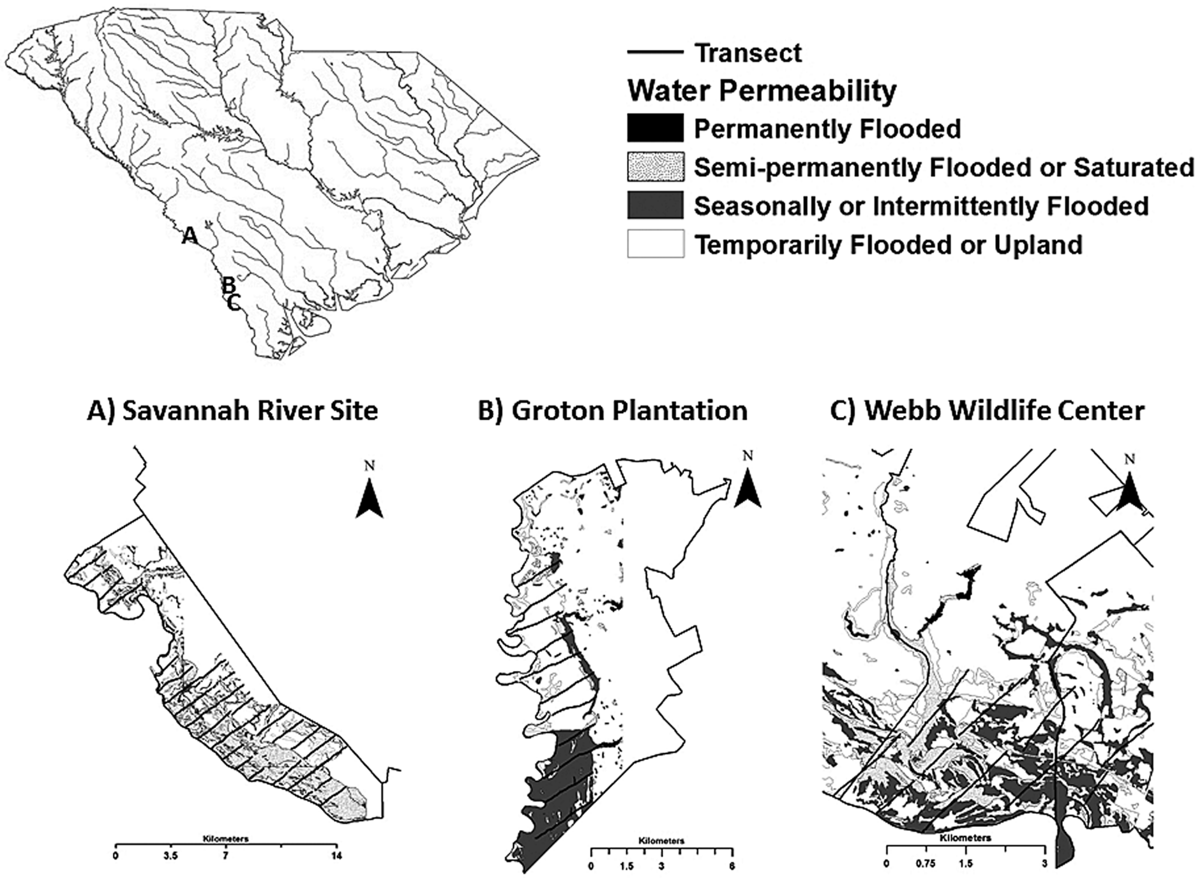

Fig. 1.—Location of 3 study sites within South Carolina and the transects established on each site for surveying for roosts of Rafinesque's big-eared bats (*Corynorhinus rafinesquii*). A = Savannah River Site, B = Groton Plantation, and C = Webb Wildlife Center. Transects at Savannah River Site were surveyed May through September 2009–2011 and transects at Groton Plantation and Webb Wildlife Center were surveyed May through September 2010–2011.

The 2,373-ha Webb Wildlife Center and Management Area (Webb) is in the Atlantic Coastal Plain Physiographic Region (Fig. 1). Approximately 39% of Webb is bottomland hardwoods with the rest made up of upland pine and hardwood forests (Boller 1992). The upland sites are actively managed through timber harvest and prescribed fire for the endangered red-cockaded woodpecker (*Picoides borealis*) and bobwhite quail (*Colinus virginianus*). Common species in the bottomlands are water tupelo, bald cypress, Carolina ash (*F. caroliniana*), red maple, hornbeam (*Ostrya virginiana*), laurel oak, willow oak (*Q. phellos*), sweetgum, and water hickory (*Carya aquatica*). No logging has occurred in the bottomlands of Webb since at least 1941 when it was acquired by the South Carolina Department of Natural Resources as a wildlife management area.

GP is a privately owned 8,900-ha site of which approximately 2,900 ha are bottomland hardwoods and swamp (Winthrop 2006). The uplands are managed primarily for quail hunting, whereas no management currently occurs in the bottomland areas. The land was most recently purchased between 1907 and 1911 when much of the bottomland forest was virgin timber. During World War II, harvesting to remove high-value commercial grade trees (i.e., high-grading) was conducted in the bottomland areas and many of the trees ≥ 66 cm in diameter at breast height (DBH) were harvested (Bonnie 2006). Additional cutting occurred in the 1970s and 1980s. Currently, much of the bottomland areas are in a conservation easement and no logging is allowed. The bottomlands consist of ridges and swales with several sloughs running through them (Kilgo 2006). The ridges are dominated by cherrybark oak, swamp chestnut oak (*Q. pagoda*), laurel oak, water oak, sweetgum, green ash, and elms (*Ulmus* spp.) with an understory of switch cane (*Arundinaria tecta*) and dwarf palmetto (*Sabal minor*). The swales are dominated by bald cypress, water tupelo, water hickory (*C. aquatica*), and overcup oak (*Q. lyrata*). Thus, the 3 sites varied in amount and time since disturbance with SRS having the most extensive and recent history of disturbance, GP having an intermediate amount of disturbance, and Webb having the least amount.

Field surveys.—At each site I established 50-m wide belt transects approximately 1 km apart and perpendicular to the floodplain (Fig. 1). Four of the transects at SRS were in the Crackerneck area just north of the main site. Two transects on SRS could not be surveyed because they were in a restricted area. A 2–4 person crew laid out the transects and conducted the surveys. Field personnel were given the starting and ending coordinates of each transect and navigated from 1 end to the other using a compass and a Trimble GEO-XT GPS

(1 m accuracy after differential correction). The transect was recorded on the GPS and the center of the transect was clearly flagged. Transects were 1.01–3.0 km in length. Each time the crew moved from 1 habitat type to another, they designated a new segment of the transect and recorded the coordinates, habitat type (e.g., cypress-tupelo, bottomland hardwood, upland hardwood, pine-hardwood, or listed dominants and co-dominants), general age (cleared or early successional, mid-successional, mature), topographic or hydrologic characteristics (water presence and depth, upland versus wetland), and obvious disturbances such as clearcutting or storm damage.

After transects and segments were established and demarcated, the crew examined all trees within 25 m of the center of the transect for the presence of basal or chimney or upper bole cavities. Although we could not examine trees with chimney or upper bole cavities, these trees were included in the survey and in some of the analyses as they represent alternate roosts. All trees with basal cavity openings were inspected but only those with cavities > 2 m high and > 30 cm wide were included in the survey as smaller cavities are unlikely to be used (Clement and Castleberry 2013). Each tree with a sufficiently large cavity was marked with a numbered aluminum tag and its location was recorded with the Trimble GEO-XT GPS unit. In most instances, 2 people inspected each cavity. Previous studies indicated that the probability of detecting Rafinesque's big-eared bats when they are present was 91–96% via inspection by 2 observers (Clement and Castleberry 2013; Fleming et al. 2013b). The species, number, and position within the cavity (low, middle, or top) of all bats were recorded as were the species, DBH, tree height, decomposition state (live or dead), inside cavity dimensions (if possible), cavity texture, and cavity opening location (basal, basal and chimney, chimney only) of each potential roost tree. Inside height and diameter of cavities with basal openings were measured with a laser distance meter and tree height was obtained using a clinometer. A rough surface was defined as > 50% of the cavity surface was covered with projections > 2 cm (Clement and Castleberry 2013). To characterize the habitat surrounding each roost, the species, DBH, and presence of cavities of all trees with a DBH of ≥ 30 cm within a 0.05-ha circular plot were recorded. Observations were done in accordance with the guidelines of the American Society of Mammalogists for the use of wild animals in research (Sikes et al. 2016).

Transects were established and trees were examined between mid-May and mid- to end September 2009–2011. The order of transect layout and inspection at each site was determined using a random number generator. Field personnel were not able to establish all of the transects during the 1st year. During 2009, 17 transects were established on SRS. During 2010, the remaining 11 transects were established on SRS, all 10 transects were established on Webb, and 8 transects were established on GP. During 2011, the remaining 3 transects were established on GP. Potential roost trees identified during the initial surveys were revisited 1–8 times. Revisits were scheduled to ensure that trees were examined throughout the field season.

Weather data were obtained from the nearest Remote Automated Weather Station (RAWS), which was located at the southern end of the SRS (33°12′38″N, 81°35′26″W). The station was approximately 14 km from the SRS study area, 52 km from the GP study area, and 70 km from the Webb study area. For each tree inspection, I determined the Julian day (JulDay), the low temperature during the previous night (PMTemp), rainfall amount (mm) during the previous night (PMRain), average daytime temperature (DayTemp), and daytime rainfall (mm; DayRain). The locations of each roost tree were imported into ArcGIS 10.0 and overlaid on the U.S. Fish and Wildlife Service National Wetland Inventory Database (http://www.fws.gov/wetlands/) to determine the wetland type for each tree location (Clement and Castleberry 2013). Trees were placed into 5 wetland classes (seasonally flooded, semi-seasonally flooded, temporarily flooded, saturated, or upland). I combined semi-seasonally and saturated sites, and temporarily flooded and upland sites in the occupancy analysis but used all 5 classes for analysis of niche breadth.

Data analysis.—A Cochran-Armitage Trend Test (SAS 9.3) was conducted to determine whether the presence of big-eared bats was related to the number of tree examinations. A Levins' standardized measure of niche breadth (B_A—Levins 1968) was used to calculate the niche breadth of roost tree species, habitat type, wetland type, roost tree DBH, and roost cavity volume for bats at SRS, GP, and Webb. Because resource availability can affect measures of niche breadth, I also calculated Smith's measure of niche breadth (Smith 1982) for roost tree species, habitat type, wetland type, roost tree DBH, and roost cavity volume at each site as well as associated 95% confidence intervals. Five size categories were created for tree DBH and cavity volumes. Categories for DBH were ≤ 70 cm, 70.1–100 cm, 100.1–130 cm, 130.1–160 cm, and > 160 cm. Categories for cavity volume were ≤ 1 m^3, 1.1–2 m^3, 2.1–4 m^3, 4.1–6 m^3, and > 6 m^3.

Rafinesque's big-eared bats switch roosts every 2–3 days (Johnson et al. 2012; Lucas et al. 2015) although they regularly return to previously used roosts (Loeb and Zarnoch 2011). Thus, it is possible that a roost may be unoccupied on any given day although it is used regularly by Rafinesque's big-eared bats. Because detection of roost use is < 1, a naïve estimator of roost occupancy that does not account for imperfect detection will underestimate use (MacKenzie et al. 2002). Thus, I treated each tree as a habitat patch and estimated probability of detection based on environmental conditions.

Although surveys were conducted over multiple years, I used a single-season occupancy model because I was not concerned with extinction or colonization and because trees are used for multiple years (Loeb and Zarnoch 2011). Further, not all trees were examined in each year. I used Program Presence (version 9.7) in a 2-stage approach to develop models of Rafinesque's big-eared bat use of trees. Data for maternity colonies and solitary individuals were combined because there is no evidence that maternity colonies and single individuals select different trees or habitats (Clement and Castleberry 2013; Lucas et al. 2015). In the 1st stage, I determined the factors that affected probability of detecting ≥ 1 Rafinesque's big-eared bat (p) which I defined as the probability of finding a bat in a tree given that the tree was used over the summer months. Few data are available on factors that affect whether a tree will be used on a particular day. Thus, I tested various environmental variables singly and in combination with Site (SRS, GP, or Webb) while holding occupancy constant. I also tested whether sampling occasion was a significant factor, as well as the null model and the global model. Environmental variables were JulDay, PMTemp, DayTemp, PMRain, and DayRain. A goodness-of-fit test was run on the global model (MacKenzie et al. 2006) which indicated that the data were not overdispersed ($\hat{c} = 1.084$, $P = 0.248$). Continuous variables were standardized using the z-transformation (e.g., JulDay, PMTemp, DayTemp) or divided by 10 (e.g., PMRain and DayRain) prior to analysis (MacKenzie 2012). The variables from the best detection model were included in subsequent occupancy models.

Seven a priori models were developed for probability of use (Ψ) based on findings from previous studies (Table 1). Because the objective was to determine whether land-use history affected roost selection, each model was run with Site as an additive term only, and as an additive and interaction term. A Pearson correlation analysis was conducted on all noncategorical variables prior to the analyses. No variables within a model were strongly correlated ($r < 0.70$). As in the detection models, continuous variables were standardized with the z-transformation but cavity volume also required a square-root transformation prior to standardization due to some exceptionally large values. A principal component analysis was conducted on tree species basal area surrounding each potential roost tree to reduce the number of variables. The first 2 components explained 91.3% of variation (72.3% and 19.6%, respectively; Supplementary Data SD1). The 1st component was heavily dominated by the presence of water tupelo, whereas the 2nd component was heavily dominated by the presence of bald cypress (Supplementary Data SD1). The principal component scores for each tree for each axis were then used in the analyses (Table 1).

An information theoretic approach was used to select the best model. Models within 2 Akaike's Information Criterion (AIC) units of the top model were considered plausible models. To examine significance of individual variables, 85% confidence limits were calculated on the parameter estimates which are appropriate in an AIC model selection approach (Arnold 2010). Means ± *SE*s of tree, cavity, and habitat characteristics are presented for used and unused trees in each site for comparison with other studies.

RESULTS

I surveyed 28 transects at SRS, 10 at Webb, and 11 at GP. I located 431 cavity trees of which 361 had basal or basal and chimney openings. Trees with basal or basal and chimney openings were examined 5.31 ± 0.08 times (range = 2–9): 6.24 ± 0.05 times at SRS, 4.54 ± 0.11 times at Webb, and 3.64 ± 0.05 times at GP. Trees with basal cavities were found on 24 of 28 transects on SRS, 7 of 10 transects on Webb, and 11 of 11 transects on GP. Big-eared bats were found in 67 (18.6%) of the trees with basal cavities and southeastern myotis were located in 12 (3.3%) cavities. Three of the trees had maternity colonies (2 on SRS and 1 on Webb). Maternity colonies contained approximately 20–35 individuals. Presence of big-eared bats was not related to the number of times a tree was examined ($z = 1.2769$, $P = 0.11$).

Mean cavity volume and tree DBH were greater in used than unused trees and greater at Webb than GP or SRS (Table 2). Further, tree density and the density and percent of large trees (i.e., > 60 cm DBH) were greater surrounding used than nonused trees and greater at Webb than at GP or SRS. Bats at Webb primarily used water tupelo and bald cypress trees as roosts, whereas bats at SRS and GP used water tupelo and bald

Table 1.—Models and associated variables used to test factors affecting roost use by Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) at 3 sites along the Savannah River Floodplain in South Carolina, United States, 2009–2011. References are the bases for inclusion of specific variables in each model. DBH = diameter at breast height.

Model	Variables	References
Management history	Site	Miles et al. (2006)
Cavity characteristics	Cavity volume	Clement and Castleberry (2013), Fleming et al. (2013a)
	Texture	Clement and Castleberry (2013)
	Opening type	Clement and Castleberry (2013)
Tree characteristics	Species (tupelo, cypress, or other)	Clement and Castleberry (2013), Johnson and Lacki (2013)
	DBH	Fleming et al. (2013a)
	Height	Trousdale (2011)
	Decomp	
Alternate roosts	% Trees with cavities	Lucas et al. (2015)
	# Large trees > 60 cm	Trousdale (2011)
	# Trees in segment	Lucas et al. (2015)
	# Trees on transect	Lucas et al. (2015)
Forest age/clutter	Total tree density	Clement and Castleberry (2013)
	% Trees > 60 cm	Arnett and Hayes (2009)
	Basal area	Gooding and Langford (2004)
Forest characteristics	Forest type	Trousdale (2011)
	Plot species composition	Lucas et al. (2015), Trousdale (2011)
Hydrology	Wetland type	Clement and Castleberry (2013)

cypress as well as a variety of other species such as blackgum (*N. sylvatica*), various species of oaks, sweetgum, hickories (*Carya* spp.), and American sycamore. Bats at SRS and GP were primarily detected in trees with basal openings, whereas bats at Webb used trees with both basal and chimney openings (Table 2). Bats at Webb used trees primarily in cypress-tupelo stands, whereas at SRS and GP approximately equal proportions of roosts were found in bottomland hardwood forests and cypress-tupelo stands. Roost trees at SRS primarily were in semi-seasonally flooded-saturated areas but were also in temporarily flooded-upland areas. Roost trees at GP were approximately equally distributed among seasonally flooded, semi-seasonally flooded-saturated, and temporarily flooded-upland sites. In contrast, bats at Webb used trees in seasonally flooded and semi-seasonally flooded-saturated areas and rarely used upland sites.

In general, bats at the more-disturbed sites (SRS and GP) exhibited the broadest niches particularly when resource availability was not considered (i.e., Levins' B_A; Table 3). When availability of resources was considered, bats at the most-disturbed site (SRS) had the broadest niches for all resources except cavity volume (Smith's FT; Table 3). However, bats at the least-disturbed site (Webb) exhibited large niches in regards to cavity volume and DBH, likely due to the greater availability of large as well as small cavities at this site compared to SRS or GP (Table 2).

The most parsimonious model explaining detection of bats in trees (p) was the one that included Site and PMRain; Site was included in all of the top models (Supplementary Data SD2). Average p was greatest at Webb (0.36), followed by GP (0.28) and SRS (0.15). The probability of detecting a Rafinesque's big-eared bat was positively related to the amount of rain that fell during the previous night. Site and PMRain were included in the subsequent occupancy models as detection covariates.

The Cavity Characteristics × Site model was the top model explaining roost occupancy by Rafinesque's big-eared bats followed by the Cavity Characteristics + Site model (Table 4). All other models had ΔAIC_c values > 34. Because the 2nd-ranked

Table 2.—Characteristics of cavities, trees, and the microhabitat surrounding trees that were used and unused as roosts by Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) on the Savannah River Site (SRS), Groton Plantation (GP), and Webb Wildlife Center (Webb). Transects at SRS were surveyed May through September 2009–2011 and transects at GP and Webb were surveyed May through September 2010–2011. DBH = diameter at breast height.

	SRS		GP		Webb	
	Used	Unused	Used	Unused	Used	Unused
Cavity volume (m^3)	4.27 ± 1.67	0.69 ± 0.05	5.81 ± 1.53	1.36 ± 0.27	14.60 ± 7.67	3.83 ± 0.80
DBH (cm)	98.73 ± 6.43	75.57 ± 4.35	140.95 ± 9.66	94.25 ± 4.14	153.62 ± 15.52	114.16 ± 7.85
Height (m)	30.58 ± 1.91	31.65 ± 0.81	40.56 ± 2.66	34.70 ± 0.98	25.25 ± 17.75	26.46 ± 1.50
% Trees with cavities	7.49 ± 1.56	6.36 ± 0.62	1.64 ± 0.84	4.91 ± 1.46	4.60 ± 1.26	6.71 ± 1.62
Basal area (m^2/ha)	114.31 ± 16.06	93.14 ± 5.93	85.72 ± 12.25	89.98 ± 13.71	357.53 ± 87.42	166.53 ± 23.62
Trees (number/ha)	406.06 ± 37.56	349.33 ± 17.02	236.67 ± 36.67	226.15 ± 15.23	441.33 ± 68.94	248.89 ± 28.93
# Trees/ha > 60 cm	125.45 ± 20.77	112.36 ± 9.19	108.89 ± 19.28	97.69 ± 8.76	262.67 ± 45.81	133.83 ± 21.09
% Trees > 60 cm	31.93 ± 3.62	30.80 ± 1.61	42.76 ± 4.38	43.30 ± 2.45	55.59 ± 6.03	52.59 ± 4.66
% Tupelo	54.6	52.8	50.0	32.1	66.7	44.4
% Cypress	18.2	7.3	11.1	7.7	26.7	19.4
% Other	27.3	39.9	38.9	60.0	6.7	36.1
% Smooth texture	84.8	65.7	83.3	59.0	86.7	50.0
% Live	84.8	91.6	100.0	97.4	80.0	94.4
% Basal only opening	81.8	92.7	83.3	94.9	33.3	66.7
% Bottomland hardwoods	51.6	44.9	55.6	75.6	6.7	19.4
% Cypress-tupelo	45.4	41.6	38.9	21.8	86.7	55.6
% Pine-upland hardwood	3.0	13.5	5.6	2.6	6.7	25.0
% Seasonally flooded	0	2.2	38.9	48.7	33.3	33.3
% Semi-seasonally flooded or saturated	75.8	62.4	27.8	20.5	60.0	44.4
% Temporarily flooded or upland	24.2	35.4	33.3	29.5	6.7	22.2

Table 3.—Levins' standardized niche breadth measure (B_A) and Smith's measure of niche breadth (FT) and 95% *CI*s of characteristics of roosts and habitats used by Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) at Savannah River Site (SRS), Groton Plantation (GP), and Webb Wildlife Center (Webb) May through September 2009–2011 in the Coastal Plain of South Carolina, United States. DBH = diameter at breast height.

Characteristic	Levins' B_A			Smith's FT		
	SRS	GP	Webb	SRS	GP	Webb
Tree species	0.237	0.149	0.086	0.887 (0.886, 0.888)	0.836 (0.834, 0.838)	0.877 (0.875, 0.879)
Tree DBH	0.848	0.571	0.664	0.923 (0.922, 0.924)	0.775 (0.772, 0.778)	0.915 (0.913, 0.917)
Cavity volume	0.735	0.750	0.481	0.890 (0.889, 0.892)	0.849 (0.846, 0.851)	0.930 (0.928, 0.931)
Forest type	0.557	0.623	0.146	0.983 (0.982, 0.983)	0.976 (0.975, 0.977)	0.969 (0.968, 0.970)
Hydrological class	0.235	0.494	0.073	0.780 (0.778, 0.782)	0.636 (0.633, 0.640)	0.612 (0.609, 0.616)

Table 4.—Number of parameters (*K*), Akaike's Information Criterion adjusted for small sample sizes (AIC_c), ΔAIC_c, and Akaike weights (ω_i) for models of roost use (Ψ) of Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) in cavity trees at the Savannah River Site, Groton Plantation, and Webb Wildlife Center in South Carolina May through September 2009–2011.

Model	*K*	AIC_c	ΔAIC_c	ω_i
Ψ(Site + CavChar + Site * CavChar), *p*(Site, PMRain)	16	650.805	0	0.613
Ψ(Site + CavChar), *p*(Site, PMRain)	10	651.724	0.919	0.387
Ψ(Site + Tree + Site * Tree), *p*(Site, PMRain)	22	685.751	34.946	0
Ψ(Site + Tree), *p*(Site, PMRain)	12	683.774	32.970	0
Ψ(Site + ForChar), *p*(Site, PMRain)	11	717.443	66.638	0
Ψ(Site + Age/Clutter), *p*(Site, PMRain)	10	717.564	66.759	0
Ψ(.), *p*(Site, PMRain)	5	718.910	68.105	0
Ψ(Site), *p*(Site, PMRain)	7	721.060	70.255	0
Ψ(Site + Hydro), *p*(Site, PMRain)	9	721.947	71.142	0
Ψ(Site + ForChar + Site * ForChar), *p*(Site, PMRain)	19	723.968	73.163	0
Ψ(Site + AltRoosts), *p*(Site, PMRain)	11	723.003	72.198	0
Ψ(Site + Age/Clutter + Site * Age/Clutter), *p*(Site, PMRain)	16	727.105	76.300	0
Ψ(Site + Hydro + Site * Hydro), *p*(Site, PMRain)	13	727.818	77.013	0
Ψ(Site + AltRoosts + Site * AltRoosts), *p*(Site, PMRain)	19	733.348	82.543	0

model was a subset of the top-ranked model, the models were not averaged. Average estimates of occupancy were 0.23 for SRS, 0.25 for GP, and 0.35 for Webb. Confidence limits on the estimates for cavity volume and the Webb × cavity volume interaction were the only ones that did not contain 0 (Table 5). Probability of occupancy increased with increasing cavity volume for bats at all sites, but pattern of use of trees with small to large cavity volumes varied across sites, most likely due to availability of trees of various sizes (Fig. 2). While occupancy of tree cavities was less than availability within the smallest size class for bats at all sites and greater than availability for the largest size class, the majority of trees occupied by bats at SRS were in the smallest size class and occupancy declined with size. In contrast, the majority of trees occupied by bats at GP were in the medium- and large-size class, and the greatest number of trees used by bats at Webb were in the largest size class.

Table 5.—Parameter estimates, unconditional *SE*s, and 85% *CI*s for the top model predicting use of roost trees by Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) at the Savannah River Site, Groton Plantation (GP), and Webb Wildlife Center (Webb) in South Carolina May through September 2009–2011. Savannah River Site was the reference site in the models.

Covariate	Estimate	*SE*	85% *CI*
Intercept	−1.094	1.178	−2.790, 0.602
GP	−0.069	3.358	−4.904, 4.766
Webb	−0.712	1.527	−2.911, 1.487
Volume	4.393	2.218	1.199, 7.587
Texture	0.739	0.714	−0.289, 1.767
Type	0.228	1.047	−1.280, 1.736
GP * Volume	−0.806	2.417	−2.674, 2.677
Webb * Volume	−3.976	2.192	−7.132, −0.820
GP * Texture	1.148	1.348	−0.793, 3.090
Webb * Texture	0.808	1.166	−0.871, 2.487
GP * Type	−2.111	3.286	−6.846, 2.618
Webb * Type	−0.820	1.374	−2.799, 1.159

DISCUSSION

Resource use and selection (i.e., disproportionate use relative to availability) are strongly dependent on resource availability, and understanding selection requires a better understanding of how animals behave across a range of habitats (Beyer et al. 2010). Land-use history such as logging or other forest management activities can greatly affect the availability of tree roosts for bats, particularly large trees with cavities (Guldin et al. 2007; Hayes and Loeb 2007; Law et al. 2015). The results of the present study indicate that occupancy of roosts by Rafinesque's big-eared bats varied across sites with different degrees and recency of disturbance. Occupancy rates decreased as disturbance increased, whereas the diversity of tree species, forest types, and wetland types used increased. Further, although Rafinesque's big-eared bats in all sites selected roosts based on cavity characteristics, especially cavity volume, this selection varied across sites.

Roost surveys are an efficient method for locating Rafinesque's big-eared bats (Clement and Castleberry 2011) and have been used successfully in a number of studies (Clement and Castleberry 2013; Fleming et al. 2013a; Lucas et al. 2015). However, Rafinesque's big-eared bats, as well as most other tree-roosting bats, switch roosts every few days (Barclay and Kurta 2007; Johnson et al. 2012; Lucas et al. 2015). Thus, it is necessary to examine roosts on multiple days before confirming whether they are being used. Using different methods, Bennett et al. (2008) and Ferrera and Leberg (2005) estimated that 3 visits are necessary to confirm that bridges are not used by Rafinesque's big-eared bats as day roosts. Clement and Castleberry (2013) and Fleming et al. (2013b) used the double-observer method to estimate the probability of detecting a bat in a roost given that it was there, and found very high detection rates (91–96%). However, their method does not account for misclassifying a roost as unused due to daily movements among roosts.

In this study, I estimated the probability of observing a bat in a roost tree over the course of 1–3 summers (sensu MacKenzie 2005). Only 1 tree had a bat in it every time that it was examined. The other 66 trees used for roosting were vacant during

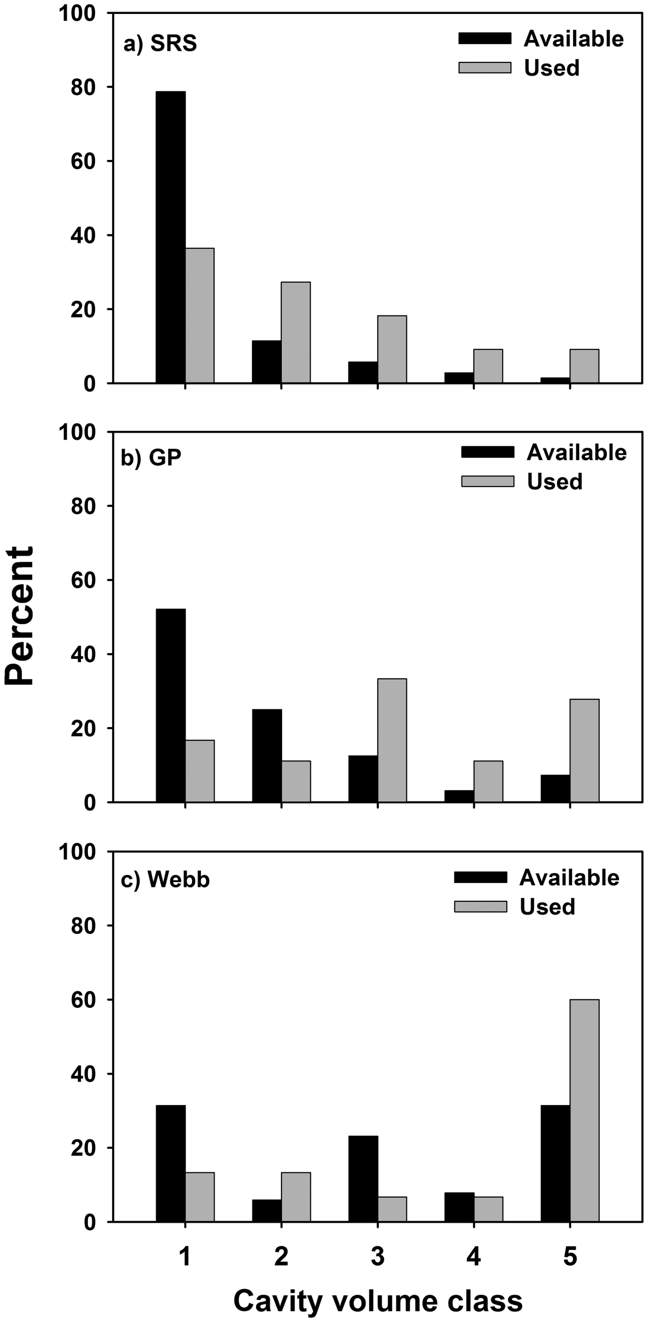

Fig. 2.—Percent of trees with basal or basal and chimney openings with cavity volumes ≤ 1 m^3 (Class 1), 1.1–2 m^3 (Class 2), 2.1–4 m^3 (Class 3), 4.1–6 m^3 (Class 4), and ≥ 6 m^3 (Class 5) that were available and used as roosts by Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) at a) Savannah River Site (SRS), b) Groton Plantation (GP), and c) Webb Wildlife Center and Management Area (Webb) May through September 2010–2011.

many of the examinations suggesting that it is necessary to examine roosts several times to document use. Further, the probability of detecting a bat in a tree varied among sites and increased with the amount of rain the previous night. Little is known about how factors such as ambient temperature and rainfall affect daily roost use of Rafinesque's big-eared bats. In a previous study at SRS, Rafinesque's big-eared bats were more likely to use artificial roosts and less likely to use tree roosts as minimum daily temperature increased in summer (Loeb and Zarnoch 2011); amount of rain during the previous night was not examined. The increased detection of bats on days following nighttime rain may be related to their seeking shelter in more protected sites such as roosts with basal openings rather than those with upper bole openings which may be more exposed to the elements. Daily radiotracking to document movements of Rafinesque's big-eared bats relative to environmental conditions would provide greater insight into the effects of temperature and rainfall on roost use and behavior of Rafinesque's big-eared bats, and could help in the design of more efficient survey methods for this species.

Probability of detecting bats also was higher at Webb than at SRS or GP. Probability of detection is often correlated with abundance or use (MacKenzie et al. 2006), which may be 1 reason why detection was greater at Webb where occupancy rates also were higher. Further, although the proportion of available trees used was greatest at Webb, the number of potential roosts and the area of bottomland hardwoods and cypress-tupelo swamp were lower than at SRS and GP. Bats at Webb may have been moving among a smaller number of trees, and thus, were more likely to be detected. Whatever the reason for differences in detection probabilities among sites, it is necessary to account for those differences as failing to do so can result in misleading conclusions about occupancy and resource selection (MacKenzie 2006).

Rafinesque's big-eared bats at all 3 sites selected roosts with greater cavity volumes. Roosts with large cavity volumes may be selected for a variety of reasons including predator evasion (Gellman and Zielinski 1996), social thermoregulation (Willis and Brigham 2007), favorable microclimates (Sedgeley 2001), and the ability to select among a variety of microclimates (Vaughan and O'Shea 1976). Clement and Castleberry (2013) concluded that selection of trees with large cavity volumes by Rafinesque's big-eared bats in the Coastal Plain of Georgia is related to predator evasion, not microclimate considerations. Although Lucas et al. (2015) did not measure cavity volumes, they also argued that roost site selection by Rafinesque's big-eared bats was related to predator avoidance based on selection for trees with large roost tree diameters (which may be correlated with cavity volume) as well as other behaviors. Larger cavities allow bats to evade predators by providing a larger flight area than smaller cavities. However, mean cavity volume of roosts used by bats at Webb was 2.5–3.4 times larger than mean cavity volume of roosts used by bats at GP or SRS, and unused cavities at Webb were 2.8–5.6 times larger than unused cavities at GP or SRS. This suggests that when very large cavities are available, bats will preferentially use them; however, when very large cavities are not available, bats are able to use cavities with smaller volumes. However, if use of roosts with large cavity volumes is necessary for predator evasion, then bats at SRS or GP may experience lower survival over time and populations may decline, as has occurred in the long-tailed bat (*Chalinolobus tuberculatus*) in managed forests of New Zealand (Borkin et al. 2011).

In addition to using trees with smaller cavity volumes, Rafinesque's big-eared bats in GP and SRS appear to have expanded their roost niches compared with bats at Webb in terms of tree species, forest type, and hydrological class. For example, although the principal component analysis indicated that tupelo and bald cypress were the dominant tree species surrounding roosts at all 3 sites, tupelo and bald cypress were the primary roost trees used by bats at Webb (93.4%), whereas these 2 species only comprised 72.8% and 61.1% of the roosts used at SRS and GP, respectively, with the rest consisting of a variety of hardwood species. Water tupelo and bald cypress are the primary roost trees used by Rafinesque's big-eared bats in 8 wildlife management areas in the Coastal Plain of Georgia (Clement and Castleberry 2013), a pristine bottomland hardwood forest in the upper Coastal Plain of South Carolina (Lucas et al. 2015), and 2 wildlife management areas in western Kentucky (Johnson et al. 2012). In contrast, tupelos comprise only 40% of roosts used by Rafinesque's big-eared bats in the DeSoto National Forest with the remaining roosts in anthropogenic structures or live or dead *Magnolia* spp. (Trousdale and Beckett 2005). Similarly, in Noxubee National Wildlife Refuge, Rafinesque's big-eared bats used a wide variety of roost tree species including black tupelo (40%), American sycamore (10%), American beech (20%), sweetgum (20%), and swamp chestnut oak (10%—Fleming et al. 2013a). DeSoto National Forest has a long history of intensive land use including logging, replacement of native forests by loblolly pine (*Pinus taeda*) plantations, and fire suppression (Trousdale et al. 2008). Prior to the 1930s when it became a refuge, considerable logging occurred in upland and bottomland habitats in Noxubee National Wildlife Refuge (U.S. Fish and Wildlife Service 2014) similar to SRS and GP. Thus, it is possible that the large variation in roost use and selection exhibited by Rafinesque's big-eared bats across their range (Trousdale 2011) may be related to past land use, particularly logging history. This suggests that consideration of an area's land-use history may be critical for predicting use and selection of roost sites by Rafinesque's big-eared bat. Further, this suggests that areas that previously contained tupelo and cypress trees but are now dominated by other bottomland hardwood species such as oaks and sweetgum should not be discounted as potential habitat for Rafinesque's big-eared bats.

Bats at SRS and GP also used roosts in a wider range of forest types and hydrological conditions than those at Webb. For example, bats at Webb used roosts in cypress-tupelo forest types almost exclusively, whereas roosts at SRS and GP were fairly evenly distributed between cypress-tupelo and bottomland hardwood forests. Expansion of roost niche breadth in disturbed forests compared with pristine forests also was observed in other bat species such as the common noctule (*Nyctalus noctula*) and Leisler's bat (*N. leisleri*) in the Białowieża Forest in Poland and Belarus (Ruczyński et al. 2010), as well as the barbastelle (*Barbastella barbastellus*) in Italy (Russo et al. 2010). In fact, the barbastelle, which was thought to depend on large snags in mature forests for roosting, recently was found using rock crevices in nonforested areas (Ancillotto et al. 2015). However, even though flexible roost behavior may allow bats to persist in disturbed areas, these areas may represent sink habitats (Pulliam 1988). For example, capture rates of barbastelles and the proportion of adult females in the population are significantly lower in managed forests compared to unmanaged forests suggesting that populations in managed forest may not be viable over the long term (Russo et al. 2010). Thus, populations in disturbed habitats may represent declining populations and local extirpation may occur if populations are not connected to source habitats or if the habitat is not restored. Very few maternity roosts were found in SRS and Webb and none at GP. Thus, it is difficult to assess the viability of populations in more-disturbed sites. Current data and future demographic studies are needed to determine if Rafinesque's big-eared bat populations in the more-disturbed sites will persist.

Results of this study suggest that Rafinesque's big-eared bats can adapt to a range of habitat conditions and disturbances by broadening their niche breadth to include more habitat types, tree and cavity sizes, and tree species. This response may be relatively common among bat species although specific examples are limited (Lacki et al. 2010; Ruczyński et al. 2010; Russo et al. 2010; Ancillotto et al. 2015). However, the limits of the adaptive responses of Rafinesque's big-eared bats are not known, and it is possible that local extirpation will occur when changes in land use result in conditions that are beyond the range of this species to adapt. Thus, studies that specifically focus on roosting behavior of bats in relation to land use, life-history strategies, social organization, and roosting strategies (e.g., crevice and foliage roosters) will provide a better understanding of how various species respond to past management activities and allow us to better predict the responses of bats to future land-use changes.

Strong selection by Rafinesque's big-eared bats of the largest cavities available exhibited in this study and others (e.g., Clement and Castleberry 2013) suggests that maintaining trees with large hollows is critical for the conservation of Rafinesque's big-eared bats in bottomland hardwood forests. Although these trees are relatively long-lived and are used for multiple years (Loeb and Zarnoch 2011), they periodically break or fall down and need to be replaced. Thus, maintaining surplus roosts by preserving all potential roost trees and ensuring that new trees are recruited into the pool of potential roosts will benefit Rafinesque's big-eared bats. Results of this study and a review of others suggest that in more pristine habitat, preservation of tupelo and bald cypress trees will be most beneficial, whereas in more-disturbed sites, preservation of large oaks, sweetgums, sycamores, and American beech as well as tupelo and cypress will be beneficial.

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Eigenvalues, percent variation explained, and factor loadings for the first 2 principal components of species composition surrounding potential roost trees for Rafinesque's big-eared bats at Savannah River Site, Webb Wildlife Center and Management Area, and Groton Plantation along the Savannah River Floodplain, South Carolina.

Supplementary Data SD2.—Number of parameters (K), Akaike's Information Criterion adjusted for small sample sizes (AIC_c), ΔAIC_c, and Akaike weights (ω_i) for models of detection probability (p) of Rafinesque's big-eared bats in cavity trees at the Savannah River Site, Groton Plantation, and Webb Wildlife Center in South Carolina May through September 2009–2011.

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