ROOSTING ECOLOGY OF RAFINESQUE'S BIG-EARED BAT AND SOUTHEASTERN MYOTIS IN THE COASTAL PLAIN OF GEORGIA

by

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(Under the Direction of Steven B. Castleberry)

ABSTRACT

Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) and southeastern myotis (*Myotis austroriparius*) roost in hollow trees in swamps in the southeastern United States, where they are designated species of concern by states throughout their range. I investigated the roosting ecology of these species, with an emphasis on structural and microclimate characteristics of roost trees and habitat characteristics affecting species abundance. I used transect searches and radio telemetry at 8 study sites across the Coastal Plain of Georgia during summer 2007 and 2008 to identify and characterize diurnal summer roost trees for both species. I found 170 Rafinesque's big-eared bat tree roosts and 25 southeastern myotis tree roosts. I analyzed the relationship between structural characteristics of hollow trees and bat presence using a single season occupancy model. Rafinesque's big-eared bats selected summer tree roosts with large cavity volumes and smooth interior walls, which is most consistent with the hypothesis that selection is related to predator evasion. Southeastern myotis tended to select water tupelo (*Nyssa aquatica*) trees with a large solid wood volume, which is most consistent with the favorable microclimate hypothesis. However, no tree structure variables were significant predictors of southeastern myotis presence, suggesting unidentified factors also affect roost selection. I placed temperature and humidity data loggers in 45 hollow trees during 2008. I used hierarchical linear and logistic models to model the relationship between tree structure and microclimate and between cavity microclimate and Rafinesque's big-eared bat presence. Tree structure variables explained <25% of variation in microclimate. Microclimate varied among available trees, but played no identifiable role in Rafinesque's big-eared bats roost selection. I modeled the relationship between number of bat colonies and landscape scale habitat variables using zero-inflated negative binomial regression. Colony density depended on duration of wetland flooding, wetland width, and study site. I generated predictive density maps to identify areas of high colony density and to estimate overall abundance. The 16,016 ha of forested wetland on the 8 study sites contained an estimated 2,190 colonies and 6,032 bats in trees with basal hollows, with density ranging from 0.04 colonies/ha in saturated wetlands to 0.27 colonies/ha in semi-permanently flooded wetlands.

INDEX WORDS: abundance, bald cypress, Coastal Plain, *Corynorhinus rafinesquii*, density, geographic information systems, Georgia, hierarchical linear model, humidity, microclimate, *Myotis austroriparius*, occupancy, Rafinesque's big-eared bat, roost selection, southeastern myotis, swamp, temperature, tree cavities, water tupelo, zero-inflated negative binomial

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INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

Bats play an important role in the health and function of forested ecosystems in North America (Marcot 1996). They consume vast numbers of insects nightly (Whitaker and Clem 1992) and are probably the primary predator of nocturnal flying insects in many areas (Williams-Guillen et al. 2008). Foraging activities of insectivorous bats likely maintain the health of natural forests as well (Kunz et al. 2011), yielding economic and cultural benefits. Bats also contribute to nutrient cycling by transporting minerals from riparian to upland areas (Marcot 1996), and even supporting rare species with their accumulated guano (Fenolio et al. 2006). Although less congenial for bats, their bodies are also sustenance to obligate parasites (Dick 2007) and food for other predators (Sparks et al. 2003). In addition to ecological benefits, bats provide economic benefits in some areas (Boyles et al. 2011). For example, bats can reduce chemical pesticide use in agricultural systems (Cleveland et al. 2006). In other contexts, bats are pollinators and seed dispersers of economically important plants (Kunz et al. 2011).

Unfortunately, given the importance of bats, populations of many forest-dwelling species have declined from historical levels (Pierson 1998, Carter et al. 2003). Recent high-profile challenges facing bat populations include mortality from white-nose syndrome (Blehert et al. 2009) and wind turbines (Kunz et al. 2007). However, the more prosaic problem of habitat loss remains a major threat to bats (Fenton 1997, Clark 2003) and for cavity roosting tree bats, suitable roosts may limit populations in some areas (Fenton 1997, Kunz and Lumsden 2003). Bottomland hardwood forests in particular are important roosting habitat for a number of bat species (Clark 2003, Carter 2006), but have declined significantly in acreage in the eastern United States (Kellison and Young 1997). Given the loss of roosting habitat, knowledge of roosting ecology of tree-dwelling bats is important for wildlife management (Miller et al. 2003).

Recent decades have seen important advances in our knowledge regarding roosts of tree bats (Brigham 2007). A synthesis of many studies suggests that tree roosting bats typically select tall, large diameter trees with low canopy cover (Kunz and Lumsden 2003, Kalcounis-Ruppel et al. 2005, Barclay and Kurta 2007). Although it has been suggested that the ultimate cause driving roost selection in bats may be predator avoidance (Ruczynski and Bogdanowicz 2005), parasite avoidance (Reckardt and Kerth 2007), or maintaining social contact (Willis and Brigham 2004), it is most commonly argued that bats select large, exposed trees because they provide a favorable microclimate supporting efficient thermoregulation (Barclay and Kurta 2007).

Despite the increase in data on tree bat roosting ecology, areas for additional study remain. First, although tree diameter and canopy cover are commonly measured to assess roost site selection by tree-roosting bats, more precise measures of tree and forest structure may provide better clues to the ultimate causes of roost selection. For example, the few studies of roost selection by cavity roosting bats that recorded internal cavity characteristics found that bat presence was more closely correlated with cavity characteristics than with diameter (Sedgeley and O’Donnell 1999, Parsons et al. 2003, Ruczynski and Bogdanowicz 2005, Willis et al. 2006). Second, despite the popularity of the hypothesis that bats select tree roosts based on microclimate, few data have been collected (Boyles 2007). Among the few North American studies that have measured roost temperatures, conclusions are divergent (Vonhof and Barclay 1997, Kalcounis and Brigham 1998, Willis and Brigham 2007). Third is a lack of abundance and distribution estimates (Kunz 2003) even though these are the fundamental building blocks of wildlife management (Krebs 1978). Underlying many of these issues is the difficulty in obtaining random samples of bats and roosts when they are cryptic and inaccessible (Willis et al. 2006).

Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) and the southeastern myotis (*Myotis austroriparius*) are tree cavity roosting bats restricted to the southeastern United States (Jones 1977, Jones and Manning 1989). In the Coastal Plain their primary natural roosts are hollow trees with basal openings in bottomlands and swamps (Harvey et al. 1999). These species are of scientific interest because they are generally considered to be uncommon (Barbour and Davis 1969), poorly studied (Harvey et al. 1999), and are designated species of concern by most states in their range (Clark 2003).

These species also present research opportunities because, among North American bats, their tree roosts are unusually conspicuous and accessible (Carver and Ashley 2008). Thus, their roosting habits create the potential for random selection of survey plots, and their accessible roosts make detailed measurements of structural and microclimate variables feasible (Sedgeley and O'Donnell 1999, Sedgeley 2001). Conspicuous roosts make it possible to differentiate unused cavities from available cavities, reducing the problem of contaminated controls (Keating and Cherry 2004, Willis et al. 2006, Barclay and Kurta 2007). Repeated surveys of randomly selected plots enable estimates of abundance from animals observed, area searched and detection probability (Williams et al. 2002). Associations between plot characteristics and abundance can also be estimated. Such abundance estimates have rarely been attempted, despite recognition of their value (Kunz et al. 2009). Therefore, I investigated the roosting ecology of Rafinesque's big-eared bat, with an emphasis on the structural and microclimate characteristics of tree cavities associated with bat presence and models of abundance and associated plot characteristics. I also studied structural characteristics of tree cavities used by southeastern myotis.

LITERATURE REVIEW

Tree Roost Structure

Rafinesque's big-eared bat and the southeastern myotis are small, insectivorous bats restricted to the southeastern United States (Jones 1977, Jones and Manning 1989). While both roost in caves (Barbour and Davis 1969, Harvey et al. 1999), they make extensive use of hollow trees in the Coastal Plain (Harvey et al. 1999). Tree roosts of both species typically are in bottomland hardwoods and baldcypress (*Taxodium distichum*) - tupelo (*Nyssa* spp.) swamps (Clark 2003). Accordingly, roosts are most commonly located in water tupelo (*N. aquatica*), and other water tolerant tree species (Clark 2003, Gooding and Langford 2004, Mirowsky et al. 2004, Carver and Ashley 2008). Additionally, roosts are located in large trees, with reported diameters at breast height (dbh) typically ≥70 cm (Clark 2003, Mirowsky et al. 2004, Gooding and Langford 2004, Carver and Ashley 2008, Stevenson 2008). While habitat, tree species, and general size of roost trees seem similar, the 2 species rarely use the same trees (Carver and Ashley 2008, Stevenson 2008), suggesting subtle niche partitioning. Differentiating the roost preferences of these species, identifying their basis for roost selection, and providing guidance for wildlife managers likely requires more refined data, including on tree cavity characteristics.

Hypotheses regarding the ultimate basis of roost selection can help guide the choice of structural characters to investigate. For example, it has been proposed that tall trees are easier for roost-switching bats to find (Brigham et al. 1997), that thick walled trees provide a more stable microclimate (Sedgeley 2001), or that large cavities have more space for roosting bats (Willis et al. 2006). Therefore, weighing the evidence that each of these structural variables is related to bat presence may illuminate the basis for roost selection and differentiate between the 2 species. The fact that the two species use the cavity space differently, with Rafinesque's big-eared bat roosting on cavity walls and southeastern myotis roosting at the cavity apex (Carver and Ashley 2008, Stevenson 2008), suggests that careful study of cavity characteristics may be more fruitful than study of external characters. Although addressed by only a few studies, cavity size and form are important characteristics of roosts for several tree-roosting species (Sedgeley and O'Donnell 1999, Parsons et al. 2003, Ruczynski and Bogdanowicz 2005, Willis et al. 2006).

Despite several successful studies of these species, knowledge gaps remain. Although both species are known to roost in caves in Georgia, a review of available records found no documented tree roosts in the state (Menzel et al. 2000). Additionally, differences in male and female roost selection have not been characterized (e.g., Carver and Ashley 2008). Furthermore, the role of structural characters of tree cavities in roost selection is unknown for these species.

Tree Roost Microclimate

Roost microclimate has been described as a "primary" and "universal" factor in roost selection by tree-roosting bats (Barclay and Kurta 2007, Boyles 2007). Presumably bats select warm and humid roosts because high roost temperature accelerate fetal development (Racey 1973, Racey and Swift 1981), milk production (Wilde et al. 1995), pup growth (Zahn 1999), and volancy (Lausen and Barclay 2006) while humid roosts moderate evaporative water loss (Webb et al. 1995). There is also empirical evidence of selection based on temperature in bat boxes (Kerth et al. 2001, Lourenco and Palmeirim 2004), rock crevice roosts (Lausen and Barclay

2003, Solick and Barclay 2006) and building roosts (Entwistle et al. 1997), with bats generally roosting in warmer structures. At least some species appear to also consider humidity in roost selection (Churchill 1991). Sedgeley (2001) reported that cavities used by the New Zealand long-tailed bat (*Chalinolobus tuberculatus*) had more stable humidity than unused cavities. That bats adjust cluster size (Trune and Slobodchikoff 1976), adjust their position within a roost (Licht and Leitner 1967) or switch roosts entirely (Hein et al. 2008) as temperature changes is further evidence for the importance of microclimate.

Despite the apparent importance of microclimate in bat roost site selection, relatively few studies have collected microclimate data for tree cavity roosts (Boyles 2007). Among those that have, the evidence has been inconsistent, suggesting that bats select warmer (Sedgeley 2001), cooler (Kalcounis and Brigham 1998), more thermally stable (Vonhof and Barclay 1997) cavities, and that bats are indifferent to cavity temperature (Willis and Brigham 2007).

In the absence of microclimate data, it has been suggested that tree structural variables may be useful proxies because the physical structure of trees should affect the internal microclimate (Vonhof and Baraclay 1996). Common features of roost trees, such as size and low canopy cover are expected to affect cavity microclimate (Kalcounis-Ruppel et al. 2005). To date, a few studies have recorded microclimate and concluded that tree size (Vonhof and Barclay 1997, Wiebe 2001) and health (Kalcounis and Brigham 1998, Wiebe 2001) affect cavity microclimate.

Despite several valuable studies, questions remain. Available studies relating tree structure to microclimate have generally occurred at higher latitudes, have rarely addressed variability within cavities, and have not specifically measured variables related to Rafinesque's big-eared bat roosts. Studies relating tree microclimate to bat presence have generated conflicting results and have not directly compared evidence for selection based on microclimate against evidence for structural variables. With low and accessible roosts, investigations of roost selection by Rafinesque's big-eared bats have high potential to address these questions.

Abundance and Distribution

Animal abundance and distribution are at the core of ecology and essential for wildlife managers (Krebs 1978). Models relating abundance to landscape features can be used to assess species status, locate areas of ecological importance, and support conservation planning and management activity (Guisan and Thuiller 2005). However, for tree-roosting bats, there are few methods for estimating abundance (Kunz et al. 2009). For example, acoustic surveys cannot identify individual bats and therefore cannot yield abundance estimates (Hayes 2000). Mist net or harp trap surveys capture a small and unknown portion of bats and thus do not yield reliable abundance estimates (Weller 2007). Furthermore, assumptions of mark-recapture models are unlikely to be met when mist-netting forest bats (Kunz et al. 2009). Particular difficulties for bat researchers are estimating the probability of capture (Thomas and West 1989) and defining the area surveyed (Weller 2007).

Theoretically, repeated roost surveys within an area could generate counts of bats, estimates of detection probabilities, and a known survey area, the elements needed for abundance estimates (Williams et al. 2002). However, bat tree roosts are typically well-hidden and roost searches for tree cavity-roosting bats have rarely been attempted (but see Sedgeley and O'Donnell 1999, Stevenson 2008, Rice 2009) and this technique has not been used to estimate population size for tree-roosting microchiroptera. Fortunately, Rafinesque's big-eared bat's accessible roosts can be surveyed directly and may yield abundance estimates.

GUIDE TO THE DISSERTATION

The dissertation is organized as a series of manuscript-style chapters addressing different aspects of the roosting ecology of Rafinesque's big-eared bat and southeastern myotis. Chapters 2 and 3 examine tree structures affecting roost site selection in Rafinesque's big-eared bat and southeastern myotis, respectively. I identified diurnal tree roosts using transect searches and radio telemetry and modeled bat presence with single season occupancy models. A manuscript based on Chapter 2 will be submitted to the *Journal of Wildlife Management*, while a manuscript based on Chapter 3 will be submitted to the *Southeastern Naturalist*.

In Chapter 4, I investigated the effect of tree structures on tree cavity microclimate and the effect of tree microclimate on presence of Rafinesque's big-eared bat. I located tree roosts with transect searches and radio telemetry and recorded tree cavity microclimate with data loggers. I modeled cavity microclimate with hierarchical linear models and I modeled bat presence with ordinary and hierarchical logistic models. This manuscript will be submitted to the Canadian Journal of Zoology. Chapter 5 addresses the abundance and density of Rafinesque's big-eared bat colonies at sites in the Coastal Plain of Georgia. I related colony abundance to large-scale habitat features using a zero-inflated negative binomial model in a geographic information system. A manuscript based on this chapter will be submitted to the *Journal of Mammalogy*.

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CHAPTER 2

SUMMER TREE ROOST SELECTION BY RAFINESQUE'S BIG-EARED BAT IN THE COASTAL PLAIN OF GEORGIA[1]

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[1] Clement, M. J. and S. B. Castleberry. To be submitted to *The Journal of Wildlife Management*.

ABSTRACT

Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) is considered rare throughout its range and is designated a species of concern by the U.S. Fish and Wildlife Service. I tested ecological hypotheses regarding roost selection by male and female Rafinesque's big-eared bats considering characteristics of trees, tree cavities, and vegetation in the immediate vicinity of trees. I used transect searches and radio telemetry at 8 study sites across the Coastal Plain of Georgia, USA to identify and characterize Rafinesque's big-eared bat diurnal summer roost sites. I searched 123 transects and radio tracked 28 bats across all study sites during 2007 and 2008. I found 173 Rafinesque's big-eared bat roosts containing approximately 870 bats. For all occupied roosts and for randomly selected unoccupied trees, I measured 15 tree characteristics and 7 plot characteristics. I analyzed hypotheses regarding the relationship between the presence of Rafinesque's big-eared bats and structural characteristics of hollow trees using a single season occupancy model and used Akaike's information criterion and Akaike weights to select the most parsimonious models. The best supported model predicted bat presence from cavity size, interior wall texture, and number of entrances. Bats selected roosts with large internal cavities (121 to 13,524 dm^3) and smooth interior walls. Because it is hypothesized that large cavities allow bats to attain evasive flight and that smooth walls impede attacks by terrestrial predators, this result was most consistent with the hypothesis that bats select roosts that allow them to evade predators that enter the roost. Because Rafinesque's big-eared bats roost in trees with characteristics that are rare across the landscape, protection of suitable wetland habitat is essential to provide current and long-term roost tree availability.

INTRODUCTION

Rafinesque’s big-eared bat (*Corynorhinus rafinesquii*) is a small, insectivorous bat restricted to the southeastern United States (Jones 1977). It commonly roosts in caves (Barbour and Davis 1969), as well as abandoned buildings (Menzel et al. 2001) and under bridges (Bennett et al. 2008). However in the Coastal Plain, Rafinesque’s big-eared bat’s primary natural roost is hollow trees (Harvey et al. 1999). It is considered uncommon throughout its range (Harvey et al. 1999) and is designated a species of concern by the U.S. Fish and Wildlife Service and state wildlife agencies. Although Rafinesque’s big-eared bat occurs in Georgia, USA, no published records of tree roosts exist for the state (Menzel et al. 2000).

Recent research indicates that tree roosts of Rafinesque’s big-eared bats typically are in bottomland hardwoods and baldcypress (*Taxodium distichum*) - tupelo (*Nyssa* spp.) swamps (Clark 2003) and near sources of water (Gooding and Langford 2004). Roosts are most commonly located in water tupelo (*N. aquatica*), but also in baldcypress and other tree species (Lance et al. 2001, Gooding and Langford 2004, Mirowsky et al. 2004, Trousdale and Beckett 2005, Carver and Ashley 2008). Additionally, roosts typically are large diameter trees, with reported mean diameters at breast height (dbh) ranging from 79 cm (Trousdale and Beckett 2005) to 155 cm (Cochran 1999). Suitable roosting habitat may have declined as bottomland hardwood forests in the Southeast have been reduced in extent by approximately 75% since pre-colonial times (Harris 1984, Fredrickson 1997).

Rafinesque’s big-eared bat roosts also are sex-segregated (England et al 1990, Trousdale and Beckett 2004), likely due to different roles and physiological needs of male and female bats during the summer (Speakman and Thomas 2003). In several bat species, sexual segregation is related to tree characteristics (Broders and Forbes 2004, Perry and Thill 2007), but such a relationship has not been evaluated for Rafinesque's big-eared bats. Sex-specific roost selection could be important because forest management techniques that are targeted towards more common bachelor roosts may not be sufficient for maternity colonies that are essential for population viability.

Although several studies have established that Rafinesque's big-eared bats roost in large diameter trees, the reason for this association is unclear. For example, it has been proposed that large trees are easier for roost-switching bats to find (Brigham et al. 1997), that large trees provide a more stable microclimate (Sedgeley 2001), or that large trees have more space for roosting bats (Evelyn et al. 2004). I attempted to distinguish between these and other roost selection hypotheses by describing cavity interiors in addition to more commonly measured exterior characteristics. I also identified differences in male and female roosts relevant to forest management.

METHODS

Study Area

Study areas included 8 sites in the Coastal Plain physiographic region of Georgia, USA (Figure 2.1). All study sites were owned or leased by the state as wildlife management areas and located within a major river floodplain with cypress-gum swamps and bottomland hardwoods as major habitat components. Study sites included Moody Forest Natural Area and Clayhole Swamp Wildlife Management Area (WMA) bordering the Altamaha River, Beaverdam and River Bend WMAs bordering the Oconee River, Ocmulgee WMA bordering the Ocmulgee River, Tuckahoe WMA bordering the Savannah River, Chickasawhatchee WMA bordering Chickasawhatchee Creek in the Flint River drainage, and Little Satilla WMA bordering the Little Satilla River. Sites were selected to achieve wide distribution across the Georgia Coastal Plain and to ensure inclusion of sites with forested cypress-gum swamp habitat across a range of ages. Study areas ranged from 1,416 ha (River Bend WMA) to 8,597 ha (Ocmulgee WMA) with area in cypress-gum swamp and bottomland hardwoods ranging from 540 ha (Moody Forest Natural Area) to 3,319 ha (Chickasawhatchee WMA). Habitat composition varied across study sites, but generally consisted of large areas of loblolly pine (*Pinus taeda*) with smaller areas of slash pine (*P. elliottii*), shortleaf pine (*P. echinata*) and hardwoods on upland sites, and cypress-gum swamps and bottomland hardwoods in areas bordering each river. At most sites, upland forests were typically <80 years old, while bottomland forests were often older.

Transect Searches

I searched for Rafinesque's big-eared bat roosts from May 11 to August 14, 2007 and May 13 to August 16, 2008. I stratified the study areas by habitat type using wetland categories defined by the US Fish and Wildlife Service's National Wetland Inventory (NWI; Cowardin et al. 1979). Given that Rafinesque's big-eared bats are found in forested wetlands (Clark 2003), I selected 3 habitat types of palustrine, forested wetland categories: saturated, seasonally flooded, and semi-permanently flooded. Saturated wetlands have saturated soil for extended periods, but surface water is rare. Seasonally flooded wetlands have surface water for extended periods early in the growing season (approximately April through October), but no surface water late in the growing season. Semi-permanently flooded wetlands have surface water during the entire growing season in most years.

I created 500 m long x 30 m wide transects along the approximate center of all wetland areas using ArcMap (version 9.2, ESRI Inc., Redlands, CA) because habitat patches were generally long and narrow. I randomly selected transects to survey at each site from each wetland category. I over-sampled semi-permanently flooded wetlands relative to their area because I anticipated this habitat type would yield more bat roosts based on reports of habitat type (Gooding and Langford 2004) and tree roost species (Trousdale and Beckett 2005). In 2007, I selected approximately 1/3 of transects from each habitat type (Table 2.1). Across the study areas, wetland types were 63% saturated wetland, 27% seasonally flooded, and 10% semi-permanently flooded. In 2008, both transects and habitat were more heavily weighted towards semi-permanently flooded habitat, with 8% of transects in saturated, 25% in seasonally flooded, and 67% in semi-permanently flooded habitat. Across the study areas, 23% was saturated, 41% seasonally flooded, and 36% semi-permanently flooded wetlands.

I conducted searches by walking the center of each transect and searching for trees with basal hollows within 15 m on each side of the transect. When a hollow tree was located, the tree was marked with flagging and the cavity was visually inspected for bats using a spotlight and mirror. It was only possible to search a tree if it had an opening of at least 3 cm by 15 cm and the opening was no more than 1.8 m from the ground. I estimated the number of bats inside each tree by counting the number of visible bats. I classified colonies with <3 bats as bachelor colonies and colonies with ≥3 bats as maternity colonies because solitary bats are typically adult males (Trousdale and Beckett 2004) and adult males rarely join maternity colonies (England et al 1990, Clark 1990). Additionally, maternity colonies were confirmed by presence of juvenile bats, identifiable by their darker pelage (Jones 1977). On the rare occasions I observed exactly two bats in a roost, neither had juvenile pelage, so I recorded them as males.

I searched transects 3 times during the same summer field season, which allowed me to calculate roost usage rates (MacKenzie et al. 2002) and reduce contaminated controls (false absences) common in use-availability studies (Keating and Cherry 2004). The first and second searches typically occurred 3 weeks apart and the third search typically occurred 5 days after the second. Additionally, I searched transects from 2007 once in 2008 to assess whether occupancy was similar between years. On the second survey, I also noted hollow trees missed on the first search to estimate rate of hollow tree detection. During the second transect search of 2008, two workers independently examined each hollow tree to estimate bat detection rate. The two observations occurred within a few minutes to ensure that each tree was closed to immigration and emigration for the duration of the two searches (MacKenzie et al. 2002). I also searched hollow trees on an ad hoc basis as they were encountered while conducting research activities.

Radio Telemetry

I captured bats using mist nets placed over creeks, sloughs, or oxbow lakes, or directly outside of known roosts. I trapped at known roosts because Rafinesque's big-eared bats are reported to be difficult to capture in mist-nets (Trousdale and Beckett 2002, Mirowsky et al. 2004). I recorded species, sex, age, reproductive condition, mass, and forearm length of captured bats and released tagged bats at the site of capture. I attached 0.4 g radio transmitters (Blackburn Transmitters, Nacogdoches, TX) to bats weighing >8.0 g and 0.3 g transmitters to bats ≤8 g (Aldridge and Brigham 1988) with Torbot Liquid Bonding Cement (Torbot Group Inc., Cranston, RI). Radio transmitters averaged 4.6% of body weight (range: 3.9 – 5.3%). I radiotagged 21 bats in 2007 and 7 bats in 2008. Capture and handling protocols were approved by the University of Georgia Institutional Animal Care and Use Committee (approval no. A2007-10046-c1) and Georgia Scientific Collecting Permit #29-WCH-06-104. I radio-tracked bats during the day, beginning the day after capture, and every day until the tag fell off, or I left the study site. I located bats using a portable telemetry receiver (TRX 2000S; Wildlife Materials Inc., Murphysboro, IL) and a 3-element Yagi antenna (Advanced Telemetry Systems, Inc, Isaanti, MI). I began each search at the last known location for the bat. If no signal was obtained, I walked along trails or roads in an increasing radius until detecting a signal. I ascertained its direction and walked toward the signal until locating the roost. If a bat was not located by late afternoon, I resumed the search the following day.

Roost-tree Quantification

I measured tree structural characteristics for every occupied tree and a subset of unoccupied trees, a design known as case-control sampling (Keating and Cherry 2004). In 2007, I measured 3 unoccupied trees per transect. Because I found most roosts in wetter habitat during the first year, I adjusted the protocol in 2008 to measure more trees in semi-permanently flooded habitat. In 2008, for every occupied tree on a site, I measured 2.5 unoccupied trees in semi-permanently flooded habitat with a minimum of 15, 0.75 unoccupied trees in seasonally flooded habitat with a minimum of seven, and 0.5 unoccupied trees in saturated habitat with a minimum of five. Once I determined the number of unoccupied trees to measure, I selected unoccupied trees at regular intervals, starting from a randomly chosen tree.

For each sampled tree, I measured diameter at breast height (dbh) using a dbh tape (Spencer Products Co., Seattle, WA) and estimated tree height using a 400LH laser hypsometer (Opti-Logic Corp., Tullahoma, TN). I counted the number of visible cavity openings on each tree and recorded distance to ground, height and width of each opening. I measured interior height of cavities using a tape measure or a hypsometer. I measured inside cavity diameter at points I could reach from the ground using a tape measure and visually estimated average diameter based on those known measurements. Cavity volume was calculated from cavity height and average diameter assuming a cylindrical shape ($h\pi r^2$). I estimated solid tree volume by subtracting estimated cavity volume from total bole volume which I estimated from bole height and dbh, assuming a conical shape ($h\pi r^2/3$). I recorded UTM coordinates of trees with an eTrex Venture HC global positioning system unit (Garmin Ltd., Olathe, KS).

I recorded species and decay state of each tree using British Columbia's Wildlife Tree Classification System (Vonhof and Barclay 1996) and recorded whether the cavity had a chimney-like opening at the top. I characterized the interior surface of the cavity as rough (>50% of cavity surface covered with projections >2 cm) or smooth and visually estimated percent of interior surface covered by fungus.

In addition to tree measurements, I established a 0.1 ha plot around selected trees and recorded the number of trees with dbh >30 cm, dbh 1-30 cm, and dbh <1 cm, counted shrub, vine, and herbaceous plant stems ≥1.4 m tall in the <1 cm dbh category, and recorded number of hollow trees within plots. I measured canopy cover by averaging readings from a convex spherical densiometer (Forest Densiometers, Bartlesville, OK) in 4 directions, taken 3 m from the tree base.

Model Development and Analysis

Hypotheses

I developed models to test the hypotheses that bat presence is affected by tree structural characteristics that influence ease of entering and exiting roosts (Sedgeley and O'Donnell 1999), ease of locating roosts (Vonhof and Barclay 1996), availability of alternative roosts (Brigham et al. 1997), distance to foraging sites (Carter 2006), predator exclusion (Ruczynski and Bogdanowicz 2005), ability to evade predators that have entered the roost (Gellman and Zielinski 1996), suitability of the roosting substrate (Siivonen and Wermendsen 2008), roost microclimate (Sedgeley 2001) or that roost usage is random relative to tree characteristics. I also developed a global model, which included all uncorrelated (Pearson $r^2 < 0.25$) predictor variables. Tree structural characteristics associated with each hypothesis were determined by a literature review (Table 2.2). Given the different behavioral and physiological constraints on males and reproductive females, and given that several studies have found differences in bachelor and maternity roost selection (e.g., Broders and Forbes 2004, Perry and Thill 2007), I included a colony type (maternity or bachelor) dummy variable and interactions between colony type (maternity or bachelor) and tree characteristics in all hypotheses. The interactions allowed the intensity of roost selection to differ by sex, but not the type of roost selection, i.e., I did not test hypotheses where females select roosts based on microclimate while males select roosts based on distance to foraging sites.

Statistical Models

I examined the relationship between presence of Rafinesque's big-eared bats and structural characteristics of hollow trees using a single season occupancy model (MacKenzie et al. 2002, MacKenzie et al. 2006). The single season occupancy model estimates probability of tree occupancy (ψ) and probability of detection (p; MacKenzie et al. 2002). However, when sites are not closed to changes in occupancy between surveys, as is the case for bat tree roosts surveyed on different days, p should be interpreted as a rate of use, rather than detection (MacKenzie and Royle 2005). Unlike logistic regression, occupancy models incorporate use rate estimates to account for potential bias due to low use rates (Tyre et al. 2003, Gu and Swihart 2004). I conducted analyses in Program MARK (White and Burnham 1999) unless otherwise noted.

In developing models of occupancy and use, I began by modeling p with a global occupancy model. I anticipated that estimates of p might be affected by bat gender, survey method (transects or radio telemetry), or time. If maternity colonies switch roosts more or less frequently than bachelors, possibly due to constraints of raising young, then *p* may be higher or lower than for bachelors. Additionally, given that roosts located by radio telemetry were only located after a bat was present, estimates of *p* might be higher. Roost use also might change through time as young bats develop and environmental conditions change through the summer. Therefore, I developed 8 models of roost use testing combinations of these factors. I used model selection procedures (described below) to select the best model of roost use and applied it to all models of roost occupancy.

When *p* at a site that is not closed is less than 1, the apparent non-use during some surveys could be because the bat is not using the site, or because the bat is present, but not detected. The apparent rate of use is the product of the actual rate of use and the detection rate. I addressed this issue by analyzing the subset of trees that were independently checked twice in one day. I estimated conditional bat detection probability (probability of detecting a bat given it is present during a survey) using another single season occupancy model (MacKenzie et al. 2002). I expected maternity colonies would be easier to detect because they have more bats available to detect. I anticipated observers might have different detection rates due to difference in experience. I expected detection probability to decrease with tree size because bats would be able to hide in large hollows. Therefore, I tested five detection probability structures with a global model of occupancy: one each that estimated detection differences by roost type, by observer, by cavity size, one that combined all three factors, and one with constant detection probability. Because this was a smaller data set, it was necessary to drop all interaction terms from the global model to obtain parameter estimates. I selected the most parsimonious probability structure, using an information-theoretic approach described below.

Before analysis, I used a natural logarithm transformation on the predictor variables “tree cavity volume” and “solid tree volume” to ensure linearity in the logit function (Hosmer and Lemeshow 2000). Each tree was included in the model twice: as a potential bachelor roost and as a potential maternity roost, which allowed me to estimate occupancy for each colony type. I calculated Pearson correlation coefficients for all pairs of predictor variables and only permitted uncorrelated variables ($r^2 < 0.25$) in the models. I considered the tree as the experimental unit for statistical analysis. A few trees located by radio telemetry had no basal hollow, so I substituted average parameter values of occupied roosts for any unmeasured internal characteristics.

Prior to hypothesis testing, I checked for a site effect in the global model to determine if pooling data from all sites was justified. If one or more study sites differed from the others after accounting for the effect of all factors hypothesized to be important, it would indicate that the hypothesized factors failed to capture all the variation and I would be unable to extrapolate the results to additional sites. A site effect could also indicate that a different model structure (e.g., hierarchical) is required. I fit an alternate global occupancy model which included a dummy variable for Little Satilla WMA because it differed the most from the other sites in tree composition with 61% of measured trees being cypress, compared to 4% on the other sites combined. I used information theoretic model selection, described below, to determine the relative support for the global models with and without a site variable and adopted the better supported model. I also estimated the total number of hollow trees on transects from the number of trees found on the first survey and new trees found during the second survey using the Moran-Zippin method (Moran 1951, Zippin 1958) to ensure that the survey protocol was adequate for locating hollow trees. This method assumes the population is closed during and between sampling periods, that sampling is random, and that probability of detecting individuals is constant in both sampling periods.

Model Selection

Once I created all the models, I used an information-theoretic approach (Burnham and Anderson 2002) to estimate the relative strength of evidence for each model corresponding to a hypothesis. I used Akaike's Information Criteria (AIC; Akaike 1973) corrected for small sample bias (AICc; Hurvich and Tsai 1989) to assess the fit of the models, with the lowest AICc indicating the best supported model. AIC is an entropy-based measure used for model comparison (Burnham and Anderson 2002). I evaluated the relative strength of evidence for each model by calculating AIC weights (w_i; Burnham and Anderson 2002). Weights can take a value from 0 to 1, with a higher value indicating greater support. I used this approach to select one of the five single season detection probability structures I tested and to select the most parsimonious of the 10 candidate occupancy models. I calculated Nagelkerke's r-square to quantify the variation explained by each model (Nagelkerke 1991).

I calculated model-averaged estimates of model coefficients and standard errors across the confidence set of models to create a composite model of roost tree use. I defined the confidence set of models as models with weight ≥10% of top model weight. I weighted each variable coefficient by AIC weights, using only those models that included the variable and rescaling the AIC weights to equal 100% across the subset of models that included the variable (Burnham and Anderson 2002). Unconditional standard errors were calculated by weighting and combining sampling variance and model selection variance for all models (Burnham and Anderson 2002). I used the composite model for inferences.

I assessed model precision by calculating 90% confidence intervals based on a *t*-statistic with *n*-1 degrees of freedom. I then transformed the log-odds β coefficients to odds ratios, which express how much more or less likely it is to achieve an outcome (e.g., bat presence) as the predictor variables change (Hosmer and Lemeshow 2000). Odds ratio confidence limits that encompass 1 indicate that estimates are not precise enough to conclusively determine the direction of the relationship between the predictor and bat occupancy. Because occupied trees were included in the data set at a higher rate than unoccupied trees, I analyzed data collected in a case-control sampling scheme (Keating and Cherry 2004). Analysis of case-control data yields unbiased estimates of β coefficients and odds ratios, although intercept terms are biased because analyzed trees are not proportional to their presence in the population (Keating and Cherry 2004). I corrected naïve occupancy estimates for a use rate <1 by summing estimated ψ for all trees to estimate the proportion of area occupied (MacKenzie et al. 2002).

Goodness of Fit

I used a parametric bootstrap procedure to evaluate the goodness-of-fit of the global roost use model, using software package RMark 1.9.7 (Laake and Rexstad 2008) in program R. In the parametric bootstrap, I fit the global model to the observed data and estimated the probability of occupancy and use for each site (tree). I calculated a measure of overdispersion, c-hat = deviance/degrees-of-freedom, for the model. A c-hat value >1 indicates a high variance, which can be due to a lack of independence between data points or a misspecified model. I then used Bernoulli trials to simulate new capture histories. Because this simulated data set is correctly specified and observations are independent, it can serve as a benchmark for comparison against the observed data. I fit the global model to the simulated data and calculated c-hat. I repeated the simulations 1000 times and compared the simulated c-hat values to the value for the observed data. I considered a c-hat for the observed data lower than >5% of the simulated c-hat values to indicate that the observed data did not suffer from problematic overdispersion.

Cross-validation

I estimated the precision of the composite model using leave-one-out cross validation for bachelor and maternity roosts separately. Cross validation estimates are nearly unbiased estimators of out-of-sample model performance (Funkunaga and Kessel 1971) and yield a measure of predictive ability without excessive variance (Efron 1983). Therefore, leave-one-out cross validation should provide an estimate of the ability of the model to estimate probability of bat presence if conditions are similar to those in this study. In leave-one-out cross validation, one data point is excluded from the sample and the occupancy analysis is repeated using the remaining data points. Results of the new analysis are used to predict presence or absence for the excluded data point and this prediction is compared to the actual state. Because occupancy analysis corrects for $p<1$, predicted presence is higher than observed presence, so we expect more prediction errors, with many sites predicted to be occupied, but with no observed occupancy. I selected a prediction cutoff equal to the prevalence of bachelor (0.272) and maternity (0.056) roosts in the data set, so that a model prediction greater than the prevalence is considered a prediction of presence. These low cutoffs reduce errors when predicting bats absent at the cost of more errors when predicting bats present. I repeated the estimation and prediction procedure for every data point and used the results to calculate prediction and classification error rates.

RESULTS

During summers 2007 and 2008 combined, I searched 1731 hollow trees on 123 transects. Of hollow trees searched, 1139 were in semi-permanently flooded, 470 were in seasonally flooded, and 122 were in saturated areas. I detected Rafinesque's big-eared bats in 122 hollow trees located on 41 transects. Additionally, I located 16 roosts during ad hoc searches and 35 via radiotracking. In total, I located 173 roosts of which 3 roosts were in abandoned buildings and 170 were in hollow trees. Of 170 tree roosts, 112 were in semi-permanently flooded, 54 were in seasonally flooded, and 4 were in saturated areas. Of the tree roosts detected, 146 roosts contained bachelor colonies and 30 contained maternity colonies (6 contained a bachelor colony and a maternity colony on different dates). I counted 142 bats in bachelor roosts and 730 bats in maternity roosts. I counted fewer bachelor bats than roosts because one radio-tracked bat could be responsible for multiple roosts. Most tree roosts were located in water tupelo (n = 147) and baldcypress (n = 12), but I also found bats in sweetgum (*Liquidambar styraciflua*; n = 3), green ash (*Fraxinus pennsylvanica*; n = 2), white oak (*Quercus alba*; n = 1), and unidentified snags (n = 5).

Occupied trees were approximately twice as large as unoccupied trees measured by either dbh or solid tree volume (Table 2.3). Cavity volume of bachelor roosts was almost five times larger than unoccupied trees and maternity roosts were ten times larger than unoccupied trees. Occupied trees also had a greater tendency to be tupelo trees, lack a rough interior, have a chimney opening, and have fewer small and medium sized trees around them. Other measured variables showed smaller differences between occupied and unoccupied trees.

Roost Selection

I located 1681 hollow trees during our first transect surveys and an additional 45 trees on the second surveys. However, the basal hollow of 23 trees had been under water during the first survey and only emerged during the second survey. Because the Moran-Zippin method assumes the population is closed, I discarded these 23 trees. Therefore, I overlooked 22 trees while at least 1703 trees had been present. The Moran-Zippin estimate of the total number of hollow trees on transects during the first survey was 1703 ± 1.1.

The alternate global model with a Little Satilla WMA dummy variable was ranked below the global model without the dummy variable, indicating a lack of study site effect. The c-hat of the global model was 1.12, which was smaller than 23.4% of the c-hat estimates from the parametric bootstrap goodness-of-fit test, indicating that overdispersion was not a problem.

The best supported model for roost use by Rafinesque's big-eared bats incorporated a radio telemetry dummy variable (Table 2.4). This model received 70% of the model weight, or 7 times the next best supported model. In this model, p for trees located by radio telemetry was 59.0%, while p for other trees was 37.7%. I used the radio telemetry model of roost use for all roost occupancy models.

The best supported detection probability structure using the data on trees surveyed twice in one day was the constant detection model (Table 2.5) which was twice as likely as the next most supported model. This model estimated detection at 95.5% in all trees indicating that the apparent roost use rate of 37.7% for non-telemetry trees was due to a use rate of 39.5% and a detection rate of 95.5%. In the set of measured trees on transects, the naïve occupancy rate was 3.1% for maternity colonies, 24.0% for bachelor colonies and 25.9% for all bats (numbers do not sum to total because a tree could be occupied by a bachelor on one day and a maternity colony on a different day). Correcting for $p<1$ indicated that the occupancy rate was actually 6.3% for maternity colonies, 32.5% for bachelor colonies and 34.0% for all bats. However, only 20% of unoccupied trees were included in the data set, so the estimated occupancy rates are 5 times too high.

The best supported model for roost occupancy by Rafinesque's big-eared bats, receiving 100% of the AICc weight, was the predator evasion model (Table 2.6). The log of tree cavity volume appeared to have the greatest effect on bat occupancy, making presence 7.02 times more likely with every unit increase (Table 2.7; Figure 2.2). The effect of rough walls was negative, making bat presence 3.66 (1/0.27) times less likely. The effect of other variables was ambiguous, with odds ratio confidence limits that included 1. Model averaging had no effect on estimates, given the large ΔAICc values. Due to the case-control sampling method, the intercepts in the figure were likely biased. An unbiased estimate would shift all lines to the right, although the magnitude of the shift was not estimated. Leave-one-out cross validation of the top model yielded many false positives, but few false absences for both male and female bats (Table 2.8).

DISCUSSION

The view that microclimate determines roost selection presently dominates the study of bat tree roosts (Barclay and Kurta 2007). This paradigm generally predicts that bats, especially reproductive females, select tree cavities that provide a warm, stable microclimate that minimizes energy expenditure (Kunz and Lumsden 2003). It is generally thought that selection for microclimate will result in bats occupying small or medium sized tree cavities in large trees (Sedgeley 2001). While the cavity must be large enough to accommodate roosting bats (Willis et al. 2006), large trees with small cavities provide the thick walls and mass that can absorb heat and provide stable cavity temperatures (McComb and Noble 1981, Vonhof and Barclay 1997, Sedgeley 2001). However, these structural features were not selected by Rafinesque's big-eared bat. Absent temperature or humidity data showing a role for microclimate in roost selection, my results do not support the hypothesis that microclimate determines roost selection by

Rafinesque’s big-eared bats in the Coastal Plain of Georgia. While many studies have concluded that bats select roosts based on their microclimates, my conclusions do not necessarily contradict other studies given the lower latitude and higher average temperatures in the Coastal Plain of Georgia relative to some other studies (e.g., Vonhof and Barclay 1996, Sedgeley and O’Donnell 1999, Willis and Brigham 2007).

Although roost microclimate may be important to roost selection for some bats, predators have the potential to impact bat populations, given bats’ low reproductive rates (Speakman 1991). My results provide compelling evidence that Rafinesque’s big-eared bat presence is best predicted by a model including large cavity volume, smooth cavity walls, and multiple cavity openings. These characters are expected to facilitate predator evasion (Gellman and Zielinski 1996, Mullin and Cooper 2002, Ruczynski and Bogdanowicz 2005).

In my results, cavity volume was the most powerful predictor of presence. Large cavities allow bats to attain evasive flight without leaving the roost (Gellman and Zielinski 1996). Rafinesque’s big-eared bats employ this strategy if disturbed, a behavior I observed while inspecting roosts. Rafinesque’s big-eared bats may be particularly well-suited to take advantage of the flight space in large cavities due to their capabilities for agile flight (Jones and Suttkus 1971). Females with pups and newly volant juveniles likely require a larger cavity to attain flight, which could explain my finding that maternity colonies were in the largest cavities. Other studies of Rafinesque’s big-eared bats have not evaluated cavity volume, but they consistently report that bats roosted in large diameter trees (Gooding and Langford 2004, Carver and Ashley 2008), which is correlated with cavity volume (Stevenson 2008).

Rough cavity surfaces had an unambiguously negative effect on occupancy. Rough surfaces enable terrestrial predators access roosting bats (Rysgaard 1942, White and Seginak

1987). Acadian flycatchers (*Empidonax virescens*) select tree roosts that are difficult for predators to climb (Mullin and Cooper 2002) and Rafinesque's big-eared bats may do the same. Openings in Rafinesque's big-eared bat roosts are low relative to other bat species (Kalcounis-Ruppell et al. 2005), which may mean they face greater selective pressure to roost in smooth-walled cavities, relative to other bat species.

Previous studies have concluded that roost tree diameter is a reliable predictor of occupancy by bats in general (Kalcounis-Ruppell et al. 2005) and Rafinesque's big-eared bats in particular (Carver and Ashley 2008, Stevenson 2008). I found that although occupied trees typically had a larger dbh than unoccupied trees, the internal characters cavity volume and rough walls were more reliable predictors of occupancy. The roost discovery model predicted that bats would occupy large dbh trees, and was the second ranked model, but it received no AICc weight. The few other bat studies that have measured tree cavity volume have often found it a better predictor of use than dbh (Gellman and Zielinksi 1996, Parsons et al. 2003, Willis et al. 2006).

In other studies where cavity volume was a reliable predictor of bat occupancy, volume has been interpreted as a proxy for other variables, such as a favorable microclimate (Sedgeley and O'Donnell 1999), a limit on colony size (Parsons et al. 2003, Willis et al. 2006), or internal flight space (Gellman and Zielinski 1996). While small cavities with thick walls may be a proxy for a stable microclimate (Sedgeley 2001), that does not appear to be the case for Rafinesque's big-eared bats that select very large cavities instead of trees with large solid wood volume. In cases where cavities are small relative to colony size, larger cavities may permit larger colonies and the attending benefits of social thermoregulation (Willis and Brigham 2007). However, it is unlikely that cavity size limited colony size in the current study because occupied cavities were over 100 times larger than those used by *Myotis* spp. in British Columbia (Parsons et al. 2003) and big brown bats (*Eptesicus fuscus*) in Saskatchewan (Willis et al. 2006). Rather, selection of roosts with very large cavities allowing flight was most consistent with the predator evasion hypothesis (Gellman and Zielinski 1996).

Given the different physiological needs of males and reproductive females, I expected they would occupy roosts with different characteristics. In other studies, bachelor and maternity roosts have differed by type (Mattson et al. 1996), stand characteristics (Broders and Forbes 2004) or elevation (Senior et al. 2005). This segregation may be due to microclimate characteristics (Broders and Forbes 2004, Perry and Thill 2007), foraging opportunities (Senior et al. 2005) or predator exclusion (Mattson et al. 1996). However, for Rafinesque's big-eared bats, the gender-cavity volume interaction term was not significant, but the lower intercept for maternity colonies indicated that maternity colonies were found in larger cavities (Table 2.3, Figure 2.2). It appears that maternity colonies containing vulnerable young selected roosts that provided the most opportunity to escape predators while bachelors occupied a greater range of roosts.

Despite differences in the number of roosts among sites, the preference for trees with large cavity volumes was consistent at all locations. Differences in number of roosts among sites were due to differences in the number of suitable roost trees available at each site, and not due to a site-specific effect. The lack of a site-specific effect across 8 study sites implies that my results regarding roost tree selection by Rafinesque's big-eared bats can potentially be applied across a wider portion of the Atlantic and Gulf Coastal Plain.

For bachelor and maternity colonies, the top model seldom classified occupied trees as unoccupied, but predicted many trees to be occupied that were never documented to be occupied. This outcome was due to the low cutoff I used in the cross-validation. This error would result in excess trees being identified as habitat, but for a species of concern, the error might be considered preferable to the alternative. Furthermore, the frequent roost switching observed suggests that some trees that were "incorrectly" predicted to be occupied could actually be occupied on other dates.

My transect survey technique, which relied on trees with basal hollows, necessarily overlooked some roost trees that lacked basal openings. Radio-tagged bats spent 33% of their days in trees without basal hollows. If these bats were representative of all Rafinesque's big-eared bats, I may have missed a third of the roosts on transects because cavity openings were not visible or were inaccessible. While my results support the hypothesis that bats occupy trees that allow them to evade predators, selective pressures may differ in trees lacking basal hollows. Bats may encounter terrestrial predators less frequently if the opening was not visible from the ground. If less visible or less accessible cavity openings provide some protection from predators, bats may tolerate smaller cavities and rougher walls in trees without basal openings.

MANAGEMENT IMPLICATIONS

Rafinesque's big-eared bats in the Coastal Plain of Georgia have specific roosting requirements that are not easily created by standard forest management practices. Roosts are most commonly found in large hollow trees with smooth interior walls. Trees with cavities >1000 dm^3 were commonly occupied by bats, and any tree with a cavity over 120 dm^3 (the smallest roost found) could be considered potential roosting habitat. Tree species used as roost trees can take many decades to >200 years to reach this size (Johnson and Beaufait 1965). It has been reported that thinning water tupelo does (Goelz et al. 2001) and does not (Kennedy 1983) increase growth rates, so appropriate silvicultural prescriptions may vary by site.

Therefore, it is essential to protect suitable wetland habitat within Rafinesque's big-eared bats range containing large trees with large cavities. To ensure long-term availability of suitable roosting habitat, forested wetland habitats with appropriate hydrologic characteristics but smaller trees should be protected to allow trees to reach the appropriate size to be used as roosts. Furthermore, given that the predator evasion hypothesis was the best supported hypothesis, management practices that affect predator populations could have implications for bat populations.

Although estimated detection rates were high for trees (99%) and bats (95%) using my survey protocol, roost use rate was considerably lower (38%). Therefore, a protocol using only a single survey would be inadequate for determining Rafinesque's big-eared bat occupancy. For similar sites, 3 or 4 surveys (MacKenzie and Royle 2005) separated by >3 days (Trousdale et al. 2008) are recommended.

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Table 2.1: Number of transects searched (Tr) and number of hectares present (Ha), by study site and habitat, during surveys for Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) roost trees in the Coastal Plain of Georgia, 2007-2008. Totals may not sum due to rounding.

Study Site	Habitat Type						Total	
	Saturated		Seasonally flooded		Semi-permanently flooded			
	Tr	Ha	Tr	Ha	Tr	Ha	Tr	Ha
2007								
Moody Forest	7	379	2	74	9	134	18	588
Ocmulgee	6	847	5	427	7	221	18	1,496
Tuckahoe	7	2,447	12	1,072	1	201	20	3,720
2008								
Beaverdam	1	1,057	3	62	7	102	11	1,221
Chickasawhatchee	2	668	6	1,220	16	2,193	24	4,080
Clayhole Swamp	1	80	3	554	8	905	12	1,540
Little Satilla	1	193	3	1,619	4	63	8	1,875
River Bend	1	167	3	499	8	158	12	824
Total	26	5,839	37	5,528	60	3,976	123	15,343

Table 2.2: Hypothesized roost selection factors, model variables, and references, for summer roosts of Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) in the Coastal Plain of Georgia, 2007-2008.

Hypothesized Roost Selection Factor	Model Variables (predicted effect)	Example Reference
Ease of ingress and egress	widest opening (+)	Constantine 1966
	highest opening (+)	Sedgeley and O'Donnell 1999
	medium trees in plot (-)	Betts 1998
Ease of discovery	height (+)	Betts 1998
	diameter (+)	Brigham et al. 1997
	canopy closure (-)	Vonhof and Barclay 1996
Availability of alternative roosts	no. hollow trees (+)	Brigham et al. 1997
	big trees in plot (+)	Brigham et al. 1997
	flooded wetland (+)	Johnson and Beaufait 1965
Distance to foraging sites	distance to water (-)	Evelyn et al. 2004
	distance to roads (-)	Perry et al 2008
	% swamp (-)	Menzel et al. 2001
Predator exclusion	widest opening (-)	Ruczynski and Bogdanowicz 2005
	lowest opening (+)	Vonhof and Barclay 1996
Predator evasion	cavity volume (+)	Gellman and Zielinksi 1996
	rough walls (-)	Mullin and Cooper 2002
	no. of openings (+)	Ruczynski and Bogdanowicz 2005
Roost substrate	rough walls (+)	Barclay et al. 1988
	chimney (-)	Siivonen and Wermendsen 2008
	fungus (-)	Parsons et al. 2003
Favorable microclimate	solid tree volume (+)	Sedgeley 2001
	canopy closure (-)	Brigham et al. 1997
	tree species (tupelo) (+)	Boyles 2007
Random	None	none
Global model	all of the above, excluding highest opening, widest opening, solid tree volume and diameter due to correlation with other predictors	All of the above

Table 2.3: Mean and standard deviations (SD) of variables measured at Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) roost trees and unoccupied trees in the Coastal Plain of Georgia, 2007-2008.

	Unoccupied Trees (n=367)		Bachelor Roosts (n=146)		Maternity Roosts (n=30)	
Variable	$\overline{X}$	SD	$\overline{X}$	SD	$\overline{X}$	SD
Tree height (m)	20.7	7.5	22.7	6.2	22.4	6.2
dbh (cm)	65.9	37.3	124.2	37.6	147.4	32.4
Cavity height (m)	3.0	2.8	7.1	3.0	8.2	2.8
Cavity diameter (cm)	26.4	17.3	57.0	19.8	78.3	20.0
Cavity volume (dm^3)	420.1	1,695.3	2,201.5	2,173.0	4,322.2	2,789.8
Solid wood volume (dm^3)	3,992	4,784	5,344	4,695	17,370	33,560
Fungus (%)	2.2	4.4	1.6	3.4	1.2	2.9
Lowest opening (cm)	13.0	28.2	48.6	156.9	179.6	275.8
Highest opening (cm)	94.9	236.0	425.7	429.4	714.5	499.7
Widest opening (cm)	31.5	24.8	46.3	29.8	49.9	20.8
No. of openings (no.)	1.7	1.3	2.5	1.8	3.2	2.4
Stems >30 cm (no.)	15.9	9.2	18.5	7.8	19.6	8.9
Stems 1 – 30 cm (no.)	135.1	132.8	78.1	79.3	48.9	36.7
Stems <1 cm (no.)	116.0	192.5	80.5	163.5	84.1	185.4
Hollow trees (no.)	1.7	1.9	1.9	1.7	2.3	1.6
Canopy cover (%)	86.2	7.3	83.4	11.2	78.3	15.7
Distance to water (m)	604.8	409.2	531.2	393.1	398.8	384.8
Distance to road (m)	429.7	404.0	409.9	346.1	307.7	234.8
Swamp landcover (%)	0.42	0.20	0.42	0.21	0.48	0.19
Semi-permanent wetland	0.57	0.49	0.64	0.48	0.83	0.37
Seasonal wetland (Y/N)	0.24	0.43	0.34	0.47	0.17	0.37
Tupelo tree (Y/N)	0.44	0.50	0.84	0.36	0.97	0.18
Live tree (Y/N)	0.89	0.32	0.94	0.24	0.97	0.18
Chimney (Y/N)	0.13	0.33	0.42	0.49	0.66	0.48
Rough interior (Y/N)	0.45	0.50	0.13	0.33	0.05	0.21

Table 2.4: Candidate set of models of roost use by Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) in the Coastal Plain of Georgia, 2007-2008. Variables, number of parameters in the model (K), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference of AIC_c between a model and the model with the lowest AIC_c (ΔAIC_c), model weights (w_i), and % of maximum w_i. All models use a global model of occupancy. Model name refers to the use probability model.

Model	K	-2Logζ	AICc	ΔAICc	w_i	% max w_i
Radio	36	1154.62	1229.19	0.00	0.697	100
Time * female	42	1145.43	1232.93	3.74	0.107	15
Time + radio	39	1152.62	1233.64	4.45	0.075	11
Female	36	1159.97	1234.54	5.35	0.048	7
Constant	35	1162.12	1234.55	5.36	0.048	7
Time * radio	42	1149.87	1237.37	8.18	0.012	2
Time + female	39	1157.48	1238.49	9.30	0.007	1
Time	38	1159.64	1238.50	9.31	0.007	1

Table 2.5: Candidate set of models used to estimate conditional bat detection probability for Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) in the Coastal Plain of Georgia, 2007-2008. Variables, number of parameters in the model (K), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference of AIC_c between a model and the model with the lowest AIC_c (ΔAIC_c), model weights (w_i), and % of maximum w_i. All models use a global model of occupancy. Model name refers to the detection probability model.

Model	K	-2Logζ	AICc	ΔAICc	w_i	% max w_i
Constant	19	177.04	216.69	0.00	0.405	100
Roost type	20	176.07	217.90	1.21	0.222	55
Observer	20	176.70	218.53	1.84	0.162	40
Volume	20	176.92	218.75	2.06	0.145	36
Type, observer, volume	22	174.09	220.31	3.62	0.066	16

Table 2.6: Candidate set of models regarding roost selection by Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) in the Coastal Plain of Georgia, 2007-2008. Variables, number of parameters in the model (K), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference of AIC_c between a model and the model with the lowest AIC_c (ΔAIC_c), model weights (w_i), and Nagelkerke's R^2. Model name refers to the hypothesis tested (Table 2.2).

Model name	K	-2Logζ	AICc	ΔAICc	w_i	R^2
Evade predators	10	1192.90	1213.10	0.00	1.000	0.432
Global	36	1154.62	1229.19	16.09	0.000	0.462
Global with site effect	37	1153.98	1230.70	17.59	0.000	0.462
Discover roosts	10	1311.55	1331.76	118.65	0.000	0.333
Microclimate	10	1344.12	1364.33	151.22	0.000	0.304
Egress and ingress	10	1366.85	1387.05	173.95	0.000	0.284
Substrate	10	1427.00	1447.21	234.11	0.000	0.226
Exclude predators	8	1467.48	1483.61	270.51	0.000	0.186
Alternate roosts	10	1521.35	1541.55	328.45	0.000	0.130
Foraging opportunities	10	1522.66	1542.86	329.76	0.000	0.128
Random	4	1537.15	1545.18	332.08	0.000	0.113

Table 2.7: Coefficient estimates, standard errors (SE), odds ratios, and odds ratio confidence limits (OR CL) for predator evasion bat occupancy model for Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) in the Coastal Plain of Georgia, 2007-2008. Italicized tree variables have confidence limits that do not include 1.

Parameter	Estimate (SE)	Odds Ratio	Upper 90% OR CL	Lower 90% OR CL
Intercept	-12.11 (1.95)			
Female	-2.94 (3.64)			
ln(volume)	*1.95 (0.32)*	*7.02*	*4.13*	*11.95*
Rough	*-1.30 (0.51)*	*0.27*	*0.12*	*0.64*
Openings	-0.05 (0.14)	1.05	0.83	1.34
Female*ln(volume)	-0.18 (0.51)	0.83	0.36	1.94
Female*rough	-0.01 (1.13)	0.99	0.15	6.44
Female*openings	-0.04 (0.19)	0.96	0.70	1.31

Table 2.8: Leave-one-out cross validation results for the best supported occupancy model for Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) presence in the Coastal Plain of Georgia, 2007-2008. Cross-validation uses a cutoff of 0.272 for male bats and 0.056 for female bats.

Known Status	Predicted Status					
	Males Present	Females Present	Both Sexes Present	Absent	Total	Classification Error
Males Present	43	0	89	8	140	5.7%
Females Present	2	0	22	0	24	0.0%
Both Present	0	1	5	0	6	0.0%
Absent	57	0	24	286	367	22.1%
Total Predictions	102	1	140	294	537	
Prediction Error	55.9%	0.0%	17.1%	2.7%		

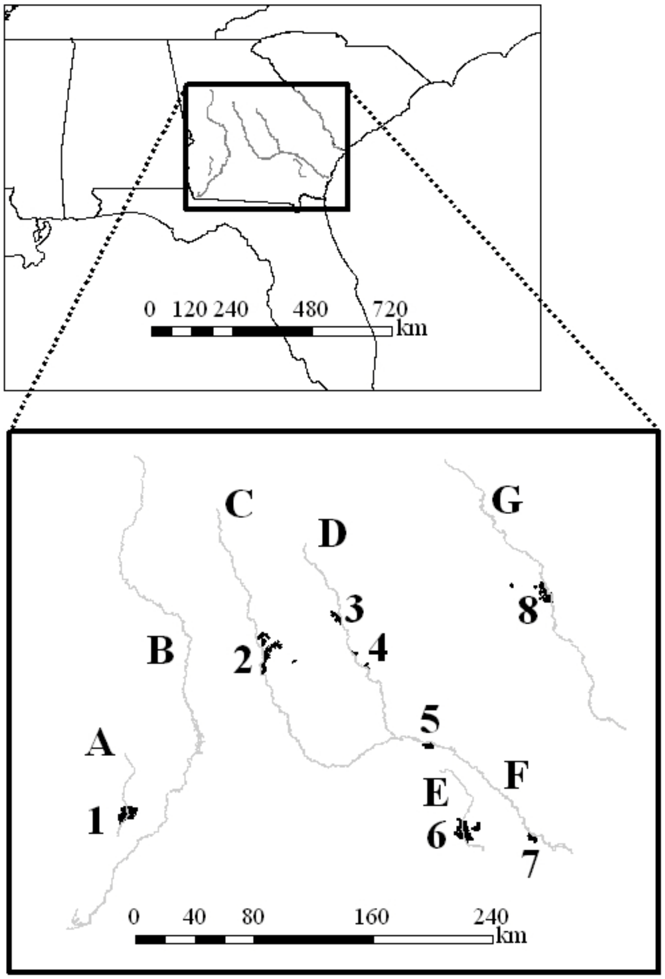

Figure 2.1: Map showing study sites and associated river systems in the Coastal Plain of Georgia, USA used to examine summer roost-site selection by Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) in 2007-2008. River systems are denoted by letters (A=Chickasawhatchee Creek, B=Flint River, C=Ocmulgee River, D=Oconee River, E=Little Satilla River, F=Altamaha River, G=Savannah River) and study sites are denoted by numbers (1=Chickasawhatchee Wildlife Management Area [WMA], 2=Ocmulgee WMA, 3=Beaverdam WMA, 4=River Bend WMA, 5=Moody Forest Natural Area, 6=Little Satilla WMA, 7=Clayhole Swamp WMA, 8=Tuckahoe WMA).

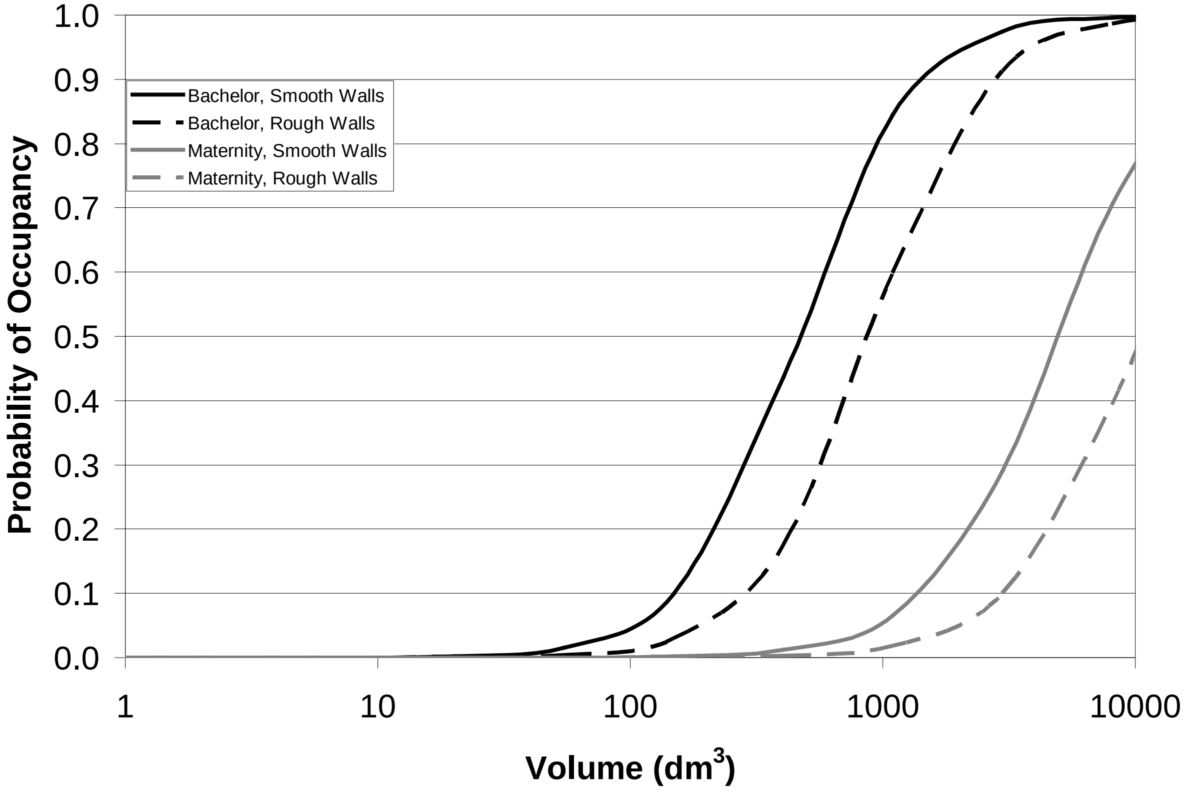

Figure 2.2: Relationship between volume and probability of occupancy by Rafinesque's big-eared bats (*Corynorhinus rafinesquii*), in the Coastal Plain of Georgia, USA under the predator evasion model. Number of entrances set to 3 for all cases shown.

CHAPTER 3

SUMMER TREE ROOST SELECTION BY SOUTHEASTERN MYOTIS IN THE COASTAL PLAIN OF GEORGIA[2]

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[2] Clement, M. J. and S. B. Castleberry. To be submitted to *The Southeastern Naturalist*.

ABSTRACT

The southeastern myotis (*Myotis austroriparius*) is a species of conservation concern, yet factors influencing selection of tree roosts by the species are poorly understood. My goal was to test hypotheses regarding roost selection by southeastern myotis considering characteristics of trees and the surrounding vegetation. I used transect searches and radio telemetry at 8 study sites across the Coastal Plain of Georgia, USA to identify and characterize southeastern myotis diurnal summer roost sites. I searched 1731 hollow trees on 123 transects and radiotracked 7 bats during 2007 and 2008 and found 25 southeastern myotis roosts containing 30 bats. For all occupied roosts and for randomly selected unoccupied trees, I measured 15 tree characteristics and 7 plot characteristics. I modeled roost tree selection with logistic regression and used Akaike's information criterion and Akaike weights to select the most parsimonious models. The best supported model indicated that bats selected water tupelo (*Nyssa aquatica*) trees with a large solid wood volume in plots with low canopy cover in Chickasawhatchee Swamp. Solid wood volume may buffer cavity microclimate, while low canopy cover likely increases solar radiation. Therefore, this result was most consistent with the hypothesis that southeastern myotis select roosts that provide a favorable microclimate. A conservative approach to leave-one-out cross-validation severely over-predicted occupied trees, but had lower error rates predicting unoccupied trees. I found more roost trees in the Dougherty Plain of Georgia than at other sites in the Coastal Plain, which may be related to the availability of cave resources. Conservation of large water tupelo trees is recommended.

INTRODUCTION

Roost trees of southeastern myotis typically are located in bottomland hardwood and baldcypress (*Taxodium distichum*) - tupelo (*Nyssa* spp.) swamps (Clark 2003) with water tupelo

(*N. aquatica*) the most commonly reported roost tree (Hoffman 1999, Hofman et al. 1999, Gooding and Langford 2004, Mirowsky et al. 2004, Carver and Ashley 2008). Roost trees generally have been characterized as large (Gooding and Langford 2004, Mirowsky et al. 2004, Stevenson 2008), but also have been reported as having smaller mean diameters compared to unoccupied hollow trees (Hoffman 1999, Carver and Ashley 2008). While studies have been conducted at several locations, the number of roosts located in most studies has been small (<9 roosts; Hoffman 1999, Hofman et al. 1999, Gooding and Langford 2004, Mirowsky et al. 2004, Carver and Ashley 2008) and no tree roosts have been documented in Georgia, USA (Menzel et al. 2000). Available roost trees may have decreased in recent centuries because bottomland hardwood acreage in the Southeast has declined in extent by approximately 75% since pre-colonial times (Harris 1984, Fredrickson 1997).

While general characteristics of southeastern myotis trees have been described, the ultimate reasons behind their choice of roosts are unknown. For example, it has been proposed that bats select roosts in hydric forest types due to increased foraging resources (Carter 2006), that taller trees are easier for roost-switching bats to find (Betts 1998), or that certain tree species provide a more favorable microclimate (Boyles 2007). One of my goals was to distinguish between these and other roost selection hypotheses.

However, most external characteristics fail to distinguish southeastern myotis roosts from sympatric Rafinesque's big-eared bat roosts (Carver and Ashley 2008). The similarity of external features combined with the fact that southeastern myotis roost on the ceilings of tree cavities, while Rafinesque's big-eared bats do not (Carver and Ashley 2008, Stevenson 2008) suggests that internal characteristics may be important in roost selection. Although few studies have measured cavity characters, cavity size and form are important for several cavity-roosting species (Sedgeley and O’Donnell 1999, Ruczynski and Bogdanowicz 2005, Willis et al. 2006, Chapter 1). Furthermore, internal characteristics are related to several roost selection hypotheses, including that large cavity size allows evasive flight (Gellman and Zielinski 1996), smooth walls inhibit predator movements (Mullin and Cooper 2002), and thick cavity walls provide a stable microclimate (Sedgeley 2001). Because southeastern myotis roosts typically have basal openings (Carver and Ashley 2008), this species is well-suited for testing hypotheses related to internal characteristics. Therefore, my objective was to test hypotheses regarding roost use by southeastern myotis, incorporating internal roost features as well as more commonly measured external tree characteristics.

METHODS

Study Area

My study areas included 8 sites in the Coastal Plain of Georgia, USA. All study sites were owned or leased by the state and located within a major river floodplain with cypress-gum swamps and bottomland hardwoods as major habitat components. Study sites included Beaverdam Wildlife Management Area (WMA), Chickasawhatchee WMA, Clayhole Swamp WMA, Little Satilla WMA, Moody Forest Natural Area, Ocmulgee WMA, Riverbend WMA, and Tuckahoe WMA. I selected sites to achieve wide distribution across the Georgia Coastal Plain and to ensure inclusion of sites with forested cypress-gum swamp habitat across a range of ages. Habitat composition varied across study sites, but generally consisted of large areas of loblolly pine (*Pinus taeda*) with smaller areas of slash pine (*P. elliottii*), shortleaf pine (*P. echinata*) and hardwoods on upland sites, and cypress-gum swamps and bottomland hardwoods in areas bordering each river. At most sites, upland forests were almost typically <80 years old, while bottomland forests were often older.

Transect Searches

I conducted searches for southeastern myotis roosts from May 11 to August 14, 2007 and May 13 to August 16, 2008. I stratified the study areas by the US Fish and Wildlife Service's National Wetland Inventory categories (NWI; Cowardin et al. 1979) because southeastern myotis are found in forested wetlands (Clark 2003). I selected 3 palustrine, forested wetland types that differ by duration of surface water: saturated, seasonally flooded, and semi-permanently flooded. I created 500 m long x 30 m wide transects along the approximate center of all wetland areas using ArcMap (version 9.2, ESRI Inc., Redlands, CA). I randomly selected transects from each wetland category to survey at each site. I over-sampled semi-permanently flooded wetlands relative to their area because I anticipated this habitat type would yield more bat roosts (Clark 2003, Gooding and Langford 2004). By combined area, the study sites were 38% saturated, 36% seasonally flooded, and 26% semi-permanently flooded while the transects were 21% saturated, 30% seasonally flooded, and 49% semi-permanently flooded

I conducted surveys by walking the length of each transect and searching for trees with basal hollows. When a basal hollow was located, I labeled it with flagging and inspected the cavity for bats using a spotlight and mirror. I estimated the number of bats by counting the number of visible bats. I searched each transect 3 times during the same summer field season because bats switch roosts frequently (Lewis 1995) and a roost that appears empty during a single survey might be used at other times. The first and second search typically occurred 3 weeks apart and the third search typically occurred 5 days after the second. I searched transects from 2007 one time in 2008 to verify no major changes had occurred. I also searched hollow trees on an *ad hoc* basis as they were encountered during research activities.

Radio Telemetry

I captured bats using mist nets placed over creeks, sloughs, or oxbow lakes, or directly outside of known roosts. I attached 0.3 g radio transmitters (Blackburn Transmitters, Nacogdoches, TX) with Torbot Liquid Bonding Cement (Torbot Group Inc., Cranston, RI). I radio-tagged bats as they were captured, with a maximum of one per night. Three bats were radio-tagged bats in 2007 and 4 in 2008. Radio transmitters averaged 4.8% of body weight (range: 4.1 – 5.3%; Aldridge and Brigham 1988). Capture and handling protocols were approved by the University of Georgia Institutional Animal Care and Use Committee (approval no. A2007-10046-c1) and Georgia Scientific Collecting Permit #29-WCH-06-104. I radio-tracked bats to day-roosts using a portable telemetry receiver (TRX 2000S; Wildlife Materials Inc., Murphysboro, IL) until the battery died, the transmitter fell off, or I moved to a new study site.

Roost-tree Quantification

I measured tree structural characteristics for every occupied tree and a subset of unoccupied trees. I measured 20% of hollow trees not occupied by bats during any search, selected at regular intervals from a random starting point. For all selected trees, I measured diameter at breast height (dbh) using a dbh tape (Spencer Products Co., Seattle, WA) and estimated tree height using a 400LH laser hypsometer (Opti-Logic Corp., Tullahoma, TN). I counted the number of visible cavity openings and recorded the distance to ground, height and width of each opening. I measured interior height of cavities using a tape measure or hypsometer. I measured inside cavity diameter at points I could reach from the ground using a tape measure and visually estimated average diameter based on those known measurements. Cavity volume was calculated from cavity height and average diameter assuming a cylindrical shape ($h\pi r^2$). I estimated solid tree volume by subtracting estimated cavity volume from total bole volume which I estimated from estimated bole height and dbh, assuming a conical shape ($h\pi r^2/3$). I recorded UTM coordinates of trees with an eTrex Venture HC global positioning system unit (Garmin Ltd., Olathe, KS).

I recorded species and decay state of each tree using British Columbia's Wildlife Tree Classification System (Vonhof and Barclay 1996) and recorded whether the cavity had a chimney-like opening. I characterized the interior surface of the cavity as rough (>50% of cavity surface covered with projections >2 cm) or smooth and visually estimated percent of interior surface covered by fungus.

I also established a 0.1 ha plot around selected trees and recorded the number of trees with dbh >30 cm, dbh 1-30 cm, and dbh <1 cm, and counted shrub, vine, and herbaceous plant stems ≥1.4 m tall in the <1 cm dbh category, and recorded number of hollow trees within plots. I measured canopy cover by averaging readings from a convex spherical densiometer (Forest Densiometers, Bartlesville, OK) in 4 directions, taken 3 m from the tree base.

Model Development and Analysis

Hypotheses

I developed models to test the hypotheses that bat presence is affected by tree structural characteristics that influence ease of entering and exiting roosts (Sedgeley and O'Donnell 1999), ease of locating roosts (Vonhof and Barclay 1996), availability of alternative roosts (Brigham et al. 1997), distance to foraging sites (Carter 2006), predator exclusion (Ruczynski and Bogdanowicz 2005), ability to evade predators that have entered the roost (Gellman and Zielinski 1996), suitability of the roosting substrate (Siivonen and Wermendsen 2008), roost microclimate (Sedgeley 2001) or that roost usage is random relative to tree characteristics. I also developed a global model, which included all uncorrelated (Pearson $r^2 < 0.25$) predictor variables. Tree structural characteristics associated with each hypothesis were determined by a literature review (Chapter 1).

Statistical Models

I examined the relationship between presence of southeastern myotis and characteristics of hollow trees using a single season occupancy model (MacKenzie et al. 2002). The single season occupancy model estimates probability of tree occupancy (ψ) and probability of detection (p). However, when sites are not closed to changes in occupancy between surveys, as is the case for bat tree roosts surveyed on different days, p should be interpreted as a rate of use, rather than detection (MacKenzie and Royle 2005). Unlike logistic regression, occupancy models incorporate use rate estimates to account for potential bias due to low use rates (Gu and Swihart 2004). I conducted analyses in Program MARK (White and Burnham 1999) unless otherwise noted.

Because southeastern myotis do not roost in chimney trees (Carver and Ashley 2008), I classified trees with chimneys as unusable habitat and removed them from the data set. Including chimney trees in the data set would result in data separation and infinite coefficient and standard error estimates. Prior to analysis, I used a natural logarithm transformation on the predictor variables “tree cavity volume” and “solid tree volume” to ensure linearity in the logit function (Hosmer and Lemeshow 2000). I calculated Pearson correlation coefficients for all pairs of predictor variables and only permitted uncorrelated variables ($r^2 < 0.25$) in the models. I considered the tree as the experimental unit for statistical analysis.

Prior to hypothesis testing, I checked for a site effect in the global model to determine if pooling data from all study sites was justified. I examined the residuals of a global logistic regression model with a one-way analysis of variance (ANOVA) for a significant effect of study site on bat presence. If the ANOVA indicated a site effect ($p < 0.10$), I determined which sites differed with a Tukey HSD *post hoc* test and fit an alternate global occupancy model which included dummy variables for all sites that differed with $p < 0.10$. I used information theoretic model selection, described below, to determine the relative support for the global models with and without site variables and then adopted the better supported study site model for all models of tree characteristics.

Model Selection

Once I created all the models, I used an information-theoretic approach (Burnham and Anderson 2002) to estimate the relative strength of evidence for each model corresponding to a hypothesis. I used Akaike's Information Criteria (AIC; Akaike 1973) corrected for small sample bias (AIC_c; Hurvich and Tsai 1989) to assess the fit of the models, with the lowest AICc indicating the best supported model. AIC is an entropy-based measure used for model comparison (Burnham and Anderson 2002). I evaluated the relative strength of evidence for each model by calculating AIC weights (w_i; Burnham and Anderson 2002). Weights can take a value from 0 to 1, with a higher value indicating greater support. I used this approach to identify the most parsimonious of the 10 candidate occupancy models. I calculated Nagelkerke's r-square to quantify the variation explained by each model (Nagelkerke 1991).

I calculated model-averaged estimates of model coefficients and standard errors across the confidence set of models to create a composite model of roost tree use. I defined the confidence set of models as models with weight ≥10% of top model weight. For the confidence set of models, I rescaled AIC weights to equal 100% and weighted each variable using the rescaled AIC weights to find the model-averaged estimates. Unconditional standard errors were calculated by weighting and combining sampling variance and model selection variance for all models (Burnham and Anderson 2002). I used the composite model for inferences.

To aid interpretation, I scaled the model-averaged coefficients for each predictor variable to a biologically relevant level, such as a 500 m change for evaluating distance to roads. I assessed model precision by calculating 90% confidence intervals based on a t-statistic with n-1 degrees of freedom. I transformed the log-odds β coefficients to odds ratios, which express how much more or less likely it is to achieve an outcome (e.g., bat presence) as the predictor variables change (Hosmer and Lemeshow 2000). Odds ratio confidence limits that encompass 1 indicate that estimates are not precise enough to conclusively determine the direction of the relationship between the predictor and bat occupancy. Because I analyzed a case-control data set, in which occupied trees were included in the data set at a higher rate than unoccupied trees, estimates of β coefficients and odds ratios were unbiased, but intercept terms were biased (Keating and Cherry 2004). I corrected naïve occupancy estimates for a use rate <1 by summing estimated ψ for all trees to estimate the proportion of area occupied (MacKenzie et al. 2002).

Goodness-of-fit and Cross-validation

I used a parametric bootstrap procedure to evaluate the goodness-of-fit of the global roost use model, using software package RMark 1.9.7 (Laake and Rexstad 2008) in program R. In the parametric bootstrap, I calculated a measure of overdispersion, c-hat = deviance/degrees-of-freedom, for the global model using the observed data. A c-hat value >1 indicates a high variance, which can be due to a lack of independence between data points or a misspecified model. I then used Bernoulli trials to simulate new capture history data, which can serve as a benchmark for comparison against the observed data. I fit the global model to 1000 sets of simulated data and calculated c-hat for each. I considered a c-hat for the observed data higher than <95% of the simulated c-hat values an indication that the observed data did not suffer from problematic overdispersion.

I estimated the precision of the best supported model using leave-one-out cross validation. Cross validation estimates are nearly unbiased estimators of out-of-sample model performance (Funkunaga and Kessel 1971) and yield a measure of predictive ability without excessive variance (Efron 1983). Therefore, leave-one-out cross validation should provide an estimate of the ability of the model to estimate probability of bat presence if conditions are similar to those in this study. In leave-one-out cross validation, one data point is excluded from the sample and the regression estimation is repeated using the remaining data points. Results of the new regression are used to predict presence or absence for the excluded data point and this prediction is compared to the actual state. I selected a prediction cutoff of 0.047, so that a model prediction ≥0.047 is considered a prediction of presence. I selected 0.047 because it was the mean probability of presence in the data set and because I assumed that wildlife managers would be more concerned with avoiding false negatives (predicting a tree is not used when it is) than other types of error. I repeated the estimation and prediction procedure for every data point and used the results to calculate prediction and classification error rates.

RESULTS

I searched 1731 hollow trees on 123 transects. I detected 22 southeastern myotis roosts during transect searches, 2 by radio tracking, and 1 during an ad hoc search. I counted 30 southeastern myotis in the roosts. Five roosts were also used by Rafinesque's big-eared bats. One tree roost was a black gum (*N. sylvatica*), while 24 were water tupelo.

On average, occupied trees were more likely to be tupelo trees and less likely to have a rough interior relative to unoccupied trees (Table 3.1). Measures of size (dbh, cavity volume, and solid wood volume) indicated that occupied trees were larger on average, but also that occupied trees tended to have less variation in size. Chimney trees made up 15% of unoccupied trees before I removed them from the data set and were never occupied by bats.

Roost Selection

The ANOVA of the logistic regression residuals indicated a strong study site effect ($F_{7,331} = 4.58$, $P<0.001$). The Tukey HSD test indicated that Chickasawhatchee differed from several other sites so I included the site dummy variable in all models. The c-hat of the global model was 0.52, which was smaller than 27.6% of the c-hat estimates from the parametric bootstrap goodness-of-fit test, indicating that there was not excessive overdispersion.

The best supported model for roost occupancy by southeastern myotis, receiving 72% of the AICc weight, was the microclimate model (Table 3.2). The predator evasion model was the only other model in the confidence set of models. The resulting composite model included six tree characters as predictor variables (Table 3.3). The site variable had the greatest effect on bat occupancy, with presence 23.3 times more likely in Chickasawhatchee. Tupelo trees were 15.0 times as likely to be occupied as other trees (Table 3.3) although confidence limits included 1. The effects of all other tree variables were weaker and ambiguous, with odds ratio confidence limits that included 1.

In the set of measured trees on transects, the naïve occupancy rate was 4.6%, while correcting for roost switching ($p = 0.57$), indicated that 6.9% of measured hollow trees were actually used. However, I only measured 20% of hollow trees, so the occupancy rate for all hollow trees would be approximately 20% as high. Leave-one-out cross validation of the composite model indicated that the classification error rate when bats were present was 20%, and

23% when bats were absent (Table 3.4). Prediction error rates were 78% when bats were predicted present, and 2% when bats were predicted absent.

DISCUSSION

The best supported hypothesis was that southeastern myotis selects roosts with a favorable microclimate. This finding is consistent with the widespread view that microclimate is the "primary factor" in roost selection by tree-roosting bats (Barclay and Kurta 2007). The hypothesis predicts that bats will select tree cavities that provide a warm, stable microclimate that minimizes energy expenditure (Kunz and Lumsden 2003). Tree structural characteristics most often associated with the hypothesis are large trees (Vonhof and Barclay 1996, Brigham et al. 1997), low canopy closure (McComb and Noble 1981, Perry and Thill 2007), and tree species (Kalcounis and Brigham 1998, Boyles 2007). Although large trees are often hypothesized to provide a favorable microclimate, there is also evidence that large cavities yield a poor microclimate due to their thin walls (McComb and Noble 1981, Sedgeley 2001) so that large trees with small cavities may provide the best microclimate.

In my results, the tree characteristic with the greatest effect on occupancy was tree species, with tupelo trees being more likely to be occupied. Other studies reported southeastern myotis roosting primarily in water tupelo (Hoffman 1999, Gooding and Langford 2004, Carver and Ashley 2008), but southeastern myotis have been documented roosting in other tree species in an area with no water tupelo (Stevenson 2008). Bats commonly appear to select certain tree species as roosts by disproportionately occupying those species (Brigham et al. 1997, Kalcounis and Brigham 1998) but the reason behind the selection is often not clear. Boyles (2007) suggested that differences in specific heat capacity of tree species may play a role in roost microclimate and therefore roost selection. Moisture content is the primary determinant of specific heat capacity in wood (Glass and Zilenka 2010) and water tupelo heartwood has higher moisture content than baldcypress and other trees encountered in the study (Glass and Zilenka 2010). Therefore water tupelo may be more thermally stable, which may explain selection of water tupelo by southeastern myotis.

Bat roost trees are commonly reported to be large dbh trees (Kalcounis-Ruppell et al. 2005), including roosts of southeastern myotis (Carver and Ashley 2008, Stevenson 2008) and they may provide a more stable microclimate (Vonhof and Barclay 1996). I expected solid wood volume to be a better predictor of microclimate than dbh because thermal conductance occurs at a constant rate and therefore a greater volume of wood will equalize surface temperatures more slowly (Glass and Zilenka 2010), while a tree with a large dbh and thin walls may be poorly buffered (Sedgeley 2001). I found that trees with a greater wood volume were more likely to be occupied, but the effect was ambiguous, with a confidence interval including 1. A number of studies have found bats roosting in areas with low canopy cover (Barclay and Kurta 2007). Canopy cover is expected to affect roost microclimate by mediating solar radiation, which heats trees and cavities (McComb and Noble 1981). I found that higher canopy cover reduced the probability of occupancy, as expected, but the effect was ambiguous, with a confidence interval including 1.

My results provide some support for the hypothesis that southeastern myotis select roosts that allow them to escape predators. In the composite model, the predator escape variable with the greatest effect was rough cavity walls, making bat presence 2.1 (1/0.48) times less likely, although the result was ambiguous. Rough surfaces allow terrestrial predators to climb towards roosting bats (White and Seginak 1987), prompting some species to avoid rough roost substrates (Mullin and Cooper 2002). Increasing cavity volume only marginally increased the probability of occupancy. For other bats, a large cavity enables them to fly and possibly avoid predators (Gellman and Zielinski 1996, Chapter 1). The weak effect of cavity volume on southeastern myotis could be because they are less agile that Rafinesque's big-eared bats (*Corynorhinus rafinesquii*; Jones and Suttkus 1971) and cannot fly within a cavity.

While some tree characteristics helped explain bat presence, the single best predictor was study site, with bats far more common in Chickasawhatchee WMA. Thus, the measured tree characteristics alone could not explain the distribution of southeastern myotis in the Coastal Plain of Georgia and an unidentified factor played an important role in bat presence. The greater number of bats at Chickasawhatchee could be related to its location in the limesink region of the Dougherty Plain (Wharton 1978). All 3 caves in Georgia known to hold southeastern myotis occur in this southwestern region, in Decatur, Grady, and Lee Counties (Scott 2011). Proximity to these cave resources may explain the higher prevalence of southeastern myotis in Chickasawhatchee. Regardless, the stark difference between sites advises caution in applying these results to other areas.

Much uncertainty remains regarding roost selection by southeastern myotis. The model averaged standard error estimates were high due to small sample size and model selection uncertainty (Burnham and Anderson 2002), resulting in ambiguous estimates of tree characteristic effects on occupancy. Additionally, the composite model had relatively poor prediction ability. A large majority of trees predicted to be occupied were unoccupied, an error which may have low costs if protecting this species of concern is a priority. However, 20% of roost trees were misclassified as unoccupied, which could leave many important roosts undetected. Greater sample sizes could alleviate some of the uncertainty.

Given that tree species was the tree characteristic best able to predict bat presence, areas suitable for water tupelo should be maintained. Water tupelo is adapted to low lying areas subject to frequent flooding and the maintenance of natural flooding regimes is essential to maintaining populations of these trees (Hook 1984). The minimum reported roost size is 23 cm dbh (Carver and Ashley 2008), and there is evidence, including this study, that very large trees are used less (Hoffman 1999, Carver and Ashley 2008). Therefore, it is important to protect suitable wetland habitat within southeastern myotis' range containing a range of tree sizes to ensure long-term availability roosts.

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Table 3.1: Mean and standard deviations (SD) of variables measured at roost trees of southeastern myotis (*Myotis austroriparious*) and unoccupied trees in the Coastal Plain of Georgia, 2007-2008.

Variable	Unoccupied trees (n=314)		Roosts (n=25)	
	$\overline{X}$	SD	$\overline{X}$	SD
Tree height (m)	21.4	7.0	24.8	4.3
dbh (cm)	63.3	34.7	93.5	30.0
Cavity volume (dm^3)	335.1	1255.6	584.7	748.5
Solid wood volume (dm^3)	3900.1	7825.8	5172.8	3925.9
Fungus (%)	2.3	4.4	2.0	2.8
Lowest opening (cm)	13.8	28.1	5.5	18.5
Highest opening (cm)	36.5	84.3	17.3	43.9
Widest opening (cm)	27.9	20.5	46.0	30.5
No. of openings (#)	1.5	1.1	1.4	0.6
Stems >30 cm (#)	17.7	9.3	19.2	8.9
Stems 1 – 30 cm (#)	132.6	131.6	74.8	40.4
No. of hollow trees (#)	1.6	1.8	2.0	1.4
Canopy cover (%)	86.0	7.6	85.9	12.3
Distance to water (m)	580.4	399.6	626.8	468.5
Distance to road (m)	427.3	410.9	496.4	428.6
Swamp landcover (%)	0.43	0.21	0.42	0.20
Semi-permanent wetland (Y/N)	0.54	0.50	0.88	0.32
Seasonal wetland (Y/N)	0.25	0.43	0.12	0.32
Tupelo tree (Y/N)	0.41	0.49	0.96	0.20
Cypress tree (Y/N)	0.06	0.24	0.00	0.00
Rough interior (Y/N)	0.48	0.50	0.04	0.20

Table 3.2: Candidate set of models regarding roost selection by southeastern myotis (*Myotis austroriparius*) in the Coastal Plain of Georgia, 2007-2008. Variables, number of parameters in the model (K), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference of AIC_c between a model and the model with the lowest AIC_c (ΔAIC_c), model weights (w_i), and Nagelkerke's R^2.

Hypothesis	Parameters	K	-2Logζ	AICc	ΔAICc	w_i	R^2
Microclimate	site[a], wood vol, cnpy, tup	6	202.96	215.21	0.00	0.715	0.347
Evade predators	site, cavity vol, rgh, open	6	204.91	217.16	1.95	0.270	0.339
Global	all	18	184.84	222.96	7.75	0.015	0.422
Discover roosts	site, hgt, dbh, cnpy	6	219.41	231.66	16.45	0.000	0.274
Substrate	site, rgh, fung	5	229.48	239.65	24.45	0.000	0.229
Egress and ingress	site, wide, high, med	6	231.32	243.57	28.36	0.000	0.220
Global, no site effect	all except site	17	210.40	246.29	31.08	0.000	0.315
Exclude predators	site, wide, low	5	239.93	250.11	34.91	0.000	0.179
Random	site	3	247.41	253.48	38.27	0.000	0.143
Alternate roosts	site, holl, big, wet	6	241.55	253.80	38.60	0.000	0.172
Foraging opportunities	site, water, rds, swamp	6	246.02	258.27	43.07	0.000	0.150

[a] site = Chickasawhatchee Wildlife Management Area, wood vol = natural log of volume of solid wood, cnpy = % canopy cover, all = all variables except cavity vol, dbh, wide and high, chim = chimney opening, rgh = rough interior walls, fung = % fungus cover, cavity vol = natural log of hollow cavity volume, open = number of openings, wide = width of widest opening, high = height of highest opening, med = number of trees with dbh 1-30 cm, hgt = tree height, dbh = diameter at breast height, holl = number of hollow trees, big = number of trees with dbh >30cm, wet = semi-permanently flooded wetland, low = height of lowest opening, water = distance to permanent water, rds = distance to road, swamp = % of area in cypress-gum swamp cover type.

Table 3.3: Model-averaged coefficient estimates, scalar, scaled odds ratios, and scaled odds ratio confidence limits (OR CL) for composite occupancy model for southeastern myotis (*Myotis austroriparius*) in the Coastal Plain of Georgia, 2007-2008. Italicized variables indicate OR CL does not include 1.

Parameter	Estimate	Scalar	Scaled Odds Ratio	Lower 90% OR CL	Upper 90% OR CL
Intercept	-11.07				
Canopy	-0.02	10	0.78	0.51	1.19
Openings	-0.12	1	0.89	0.62	1.26
Rough	-0.73	1	0.48	0.07	3.14
Site	*3.15*	*1*	*23.32*	*7.64*	*71.19*
Tupelo	2.71	1	15.03	0.74	304.65
ln(Cavity volume)	0.25	1	1.28	0.70	2.35
ln(Wood volume)	0.78	1	2.18	0.87	5.48

Table 3.4: Leave-one-out cross validation results for the composite occupancy model of southeastern myotis (*Myotis austroriparius*) presence in the Coastal Plain of Georgia, 2007-2008.

Known Status	Predicted Status			
	Present	Absent	Total	Classification Error
Present	20	5	25	20.0%
Absent	72	242	314	22.9%
Total Predictions	92	247	339	
Prediction Error	78.3%	2.0%		

CHAPTER 4

INFLUENCE OF MICROCLIMATE ON RAFINESQUE'S BIG-EARED BAT ROOST SELECTION[3]

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[3] Clement, M. J. and S. B. Castleberry. To be submitted to the *Canadian Journal of Zoology*.

ABSTRACT

It has been widely hypothesized that cavity-roosting bats select tree roosts based on microclimate characteristics and tree structure variables have been suggested as useful proxies for cavity microclimate. Although many studies have related tree structure to bat presence, few have quantified cavity microclimate and estimated the relationship between tree structure and microclimate or between microclimate and bat presence. I placed temperature and humidity data loggers in 45 hollow trees, including 28 used as roosts by Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) from May to August 2008. I used hierarchical linear models to model the relationship among tree structure and microclimate and between locations within a cavity and microclimate gradients. I used logistic regression and hierarchical logistic models to model the relationship between cavity microclimate and bat presence. Hierarchical linear models indicated that tree structure variables explained <20% of variation in microclimate among trees and <5% of variation in microclimate gradients within trees. Microclimate did not distinguish between used and unused cavities, although the data provided qualified support for the conclusion that warmer roosts were used on more days than cooler roosts. While Rafinesque's big-eared bats select tree roosts with large cavity volumes, my data indicate that the selection is driven by predators or other factors unrelated to microclimate.

INTRODUCTION

Roost microclimate is commonly thought to be the primary factor in roost selection by tree-roosting bats (Barclay and Kurta 2007). Given that higher roost temperatures accelerate fetal development (Racey 1973, Racey and Swift 1981), milk production (Wilde et al. 1995), pup growth (Zahn 1999), and volancy (Lausen and Barclay 2006), there is reason to expect bats to select high temperature roosts. Additionally, humid roosts may reduce evaporative water loss

(Webb et al. 1995) which could be important to reproductive females (Kurta et al. 1990). Studies of roost selection have demonstrated selection based on temperature in bat boxes (Kerth et al. 2001, Lourenco and Palmeirim 2004), rock crevice roosts (Lausen and Barclay 2003, Solick and Barclay 2006) and building roosts (Entwistle et al. 1997), with bats generally roosting in structures that are warmer than unused structures. Behavioral studies have also shown that roosting bats are sensitive to temperature, with bats adjusting cluster size (Trune and Slobodchikoff 1976), adjusting their position within a roost (Licht and Leitner 1967) or switching roosts entirely (Hein et al. 2008) as temperatures change. Fewer studies have examined humidity in natural roosts, especially tree roosts, but at least some species appear to select humid sites for roosts (Churchill 1991).

For tree cavity roosts, much of the evidence is more indirect. Because bats often roost in tall, dead trees (Barclay and Kurta 2007), assessing cavity microclimate directly can be logistically difficult. A common alternative approach is to assume that tree structure affects microclimate and then measure structure as a proxy for microclimate (Boyles 2007). For example, lower canopy cover should allow more solar radiation yielding a higher temperatures, while greater tree size should buffer internal climate against external changes. Thus, the trend among tree roosting bats to select large trees with low canopy cover (Kalcounis-Ruppel et al. 2005) often is interpreted as indirect support for a relationship between microclimate and bat presence (Barclay and Kurta 2007).

The interpretation that selection of tree structures indicates selection of roost microclimate requires a predictable relationship between tree characteristics and roost microclimate. However, tree and forest structure are multidimensional, so the relationship between structure and microclimate may be too complicated to accurately predict. Furthermore, evidence from studies relating cavity structure and microclimate is mixed, with studies concluding that tree size does (Wiebe 2001) or does not (Coombs et al. 2010) affect cavity microclimate. Therefore, the expectation that microclimate can be deduced from tree characters, such as diameter and canopy cover, needs to be tested with cavity microclimate data (Boyles 2007).

Even if there is a close relationship between tree structure and microclimate, differences among roosts may not be biologically significant. For example, microclimate differences among tree cavities may not be large enough to significantly impact energy consumption. A 1 °C increase in temperature in brown long-eared bat (*Plecotus auritus*) roosts in Scotland decreased roosting energy expenditure by <4% (Entwistle et al. 1997), which may or may not affect fitness. Even if there are microclimate differences among trees, large microclimate differences within tree roosts may allow bats to adjust their microclimate via roost positioning (Vaughn and O’Shea 1976) rather than roost selection. Therefore, establishing the magnitude of variation within and between roosts is important for establishing the potential for roost selection.

Few studies have compared microclimates between occupied and unoccupied tree cavities (Boyles 2007). Results of those studies are contradictory, finding that bats select warmer cavities (Sedgeley 2001), cooler cavities (Kalcounis and Brigham 1998), more thermally stable cavities (Vonhof and Barclay 1997), or that bats are indifferent to cavity temperature (Willis and Brigham 2007). Therefore, the hypothesis that bats select tree roosts based on microclimate requires further testing with bat presence and microclimate data (Boyles 2007).

Rafinesque’s big-eared bat (*Corynorhinus rafinesquii*) is a small, insectivorous bats restricted to the southeastern United States (Jones 1977). In the Coastal Plain, summer roosts typically are in large diameter hollow trees in baldcypress (*Taxodium distichum*) - tupelo (*Nyssa* spp.) swamps (Gooding and Langford 2004). Preferred roosts have large cavities with smooth interior walls (Chapter 1). This species is unusual among North American tree roosting bats for using trees with basal hollows (Carver and Ashley 2008), which makes it feasible to monitor cavity microclimate as well as use by bats. That these bats use large cavities with thin walls suggests they do not select cavities with buffered microclimates, contravening common hypotheses for cavity roosting bats, but microclimate data are lacking. My objective was to test hypotheses about the role of tree cavity microclimate in tree roost selection. Specific hypotheses evaluated were that (1) tree structural characteristics affect cavity microclimate, (2) position within large cavities affects microclimate, (3) microclimate affects which trees are used as roosts during the summer, and (4) microclimate affects the days on which suitable roost trees are used.

METHODS

Study Area

I collected data in the Coastal Plain physiographic region of Georgia at Beaverdam Wildlife Management Area (WMA), Chickasawhatchee WMA, Clayhole Swamp WMA, Little Satilla WMA, and River Bend WMA. I selected sites expected to contain roosts of Rafinesque's big-eared bats due to the presence of large areas of cypress-gum swamps and bottomland hardwoods, as ascertained from maps and site visits. Habitat composition varied across study sites, but upland areas were generally populated by large areas of loblolly pine (*P. taeda*) with smaller areas of slash pine (*P. elliottii*), shortleaf pine (*P. echinata*), and upland hardwoods, while low-lying areas contained cypress-gum swamps and bottomland hardwoods. At most sites, upland forests were almost entirely <80 years old, while bottomland forests were often older.

Field Data Collection

I located 871 hollow trees containing 65 tree roosts of Rafinesque's big-eared bat across all sites during the summer of 2008 using transect searches and *ad hoc* searches of hollow trees, as well as radio telemetry of captured bats (Chapter 1). Between May 21 and August 16, 2008, I placed 11 temperature and relative humidity data loggers in selected trees (7 HOBO Pro-V2 U23 Loggers and 4 HOBO H08 Loggers, Onset Computer Corporation, Pocasset, Massachusetts). Data loggers were attached to PVC pipe and positioned inside each tree 1.5 m above the ground, where they recorded tree cavity temperature and relative humidity (hereafter, microclimate) every hour. At each study site, I placed a data logger in every occupied tree until all data loggers were in use. Additionally, I paired every occupied tree with the closest unoccupied tree with a cavity volume >50 dm^3, the minimum roost size. I also attached a single data logger to the exterior of a tree in a shaded location to record ambient temperature and humidity. I visited all active data loggers daily and recorded the number and species of bats present. After two to three weeks, I moved to a new study site and repeated the process.

I calibrated the data loggers by placing them together in one location for 3 days before and again after the data collection period. I assumed the mean reading from all data loggers during the calibration period equaled the true microclimate, and that the mean difference between a data logger and the overall mean was the bias of that data logger. I subtracted the bias of each data logger from all its measurements and used this calibrated value for all calculations.

In addition to microclimate data, I recorded tree species, dbh, number of visible openings, and whether a chimney opening was present. I characterized the interior surface of the cavity as rough (>50% of cavity surface covered with projections >2 cm) or smooth. I measured canopy cover by averaging readings from a convex spherical densiometer (Forest Densiometers, Bartlesville, OK) in 4 directions, taken 3 m from the tree base. I measured cavity height and diameter with a measuring tape and calculated cavity volume assuming a cylindrical shape ($h\pi r^2$). I estimated solid tree volume by subtracting estimated cavity volume from total bole volume which I estimated from bole height and dbh, assuming a conical shape ($h\pi r^2/3$).

I examined microclimate gradients within 2 individual trees by placing 2 data loggers at 1 and 3.5 m above the ground against the north cavity wall and 2 data loggers at the same heights on the south cavity wall. Data loggers were held in place against the cavity wall with mesh fabric, and protected by a perforated plastic hemisphere. An additional data logger was attached to a 1.5 m length of PVC pipe, as in other trees. Temperature and humidity data were collected between June 25 and August 4, 2010. Both trees monitored by 5 data loggers were known Rafinesque's big-eared bat roosts, but were not surveyed for bats during the data collection period.

Model Development and Analysis

Factors Affecting Roost Microclimate

It is often hypothesized that solar radiation and air convection interact with structural tree properties to determine microclimate within trees (Boyles 2007). A literature review identified tree structures most commonly hypothesized to affect microclimate, such as dbh and canopy cover (Table 4.1). In addition to tree structure, I expected roost microclimate might be affected by ambient climate (McComb and Noble 1981, Coombs et al. 2010) and number of bats present (Burnett and August 1981, Willis and Brigham 2007).

Although there was a natural hierarchical structure to the data, with observations nested within trees, I considered ordinary linear regression models, because they are parsimonious if the assumption of independent error terms is met. I examined the model residuals, grouped by tree, for linear regression models and found that residuals differed by tree, indicating dependence in the error terms (Figure 4.1). Therefore, I modeled cavity microclimate as a function of tree structure using hierarchical linear models (HLMs; Raudenbush and Bryk 2002). HLMs are appropriate when observations, and therefore their error terms, are not independent, in this case repeated temperature readings from a set of trees. HLMs account for non-independent error terms by including random effects which model the dependency of observations from a related group (e.g., tree) (Raudenbush and Bryk 2002). A 2-level HLM requires a separate level 1 model of the dependent variable (e.g., maximum temperature) for each of *j* level 2 units (trees). The level 1 models take the form:

$$Y_{ij} = \beta_{0j} + \beta_{1j}*X_{1ij} + \beta_{2j}*X_{2ij} + \beta_{3j}*X_{3ij} + e_{ij} \qquad (1)$$

where Y_{ij} is the dependent variable (e.g., maximum temperature) at time *i* in tree *j*, β_{0j} is the intercept for tree *j*, the X's are level 1 predictors (e.g., ambient climate), the β's are the coefficients for the X predictors, and e_{ij} is an error term which is assumed to be normally distributed with mean 0 and variance σ^2 within each level 2 unit. If conditions differ within each unit, the β's may differ among units. The level 2 models seek to explain these differences by treating the level 1 regression coefficients as dependent variables related to level 2 predictors. The level 2 models take the form:

$$\beta_{0j} = \gamma_{00} + \gamma_{01}*W_{1j} + \gamma_{02}*W_{2j} + u_{0j} \qquad (2)$$

$$\beta_{1j} = \gamma_{10} + \gamma_{11}*W_{1j} + \gamma_{12}*W_{2j} + u_{1j} \qquad (3)$$

$$\beta_{2j} = \gamma_{20} + \gamma_{21}*W_{1j} + \gamma_{22}*W_{2j} + u_{2j} \qquad (4)$$

$$\beta_{3j} = \gamma_{30} + \gamma_{31}*W_{1j} + \gamma_{32}*W_{2j} + u_{3j} \qquad (5)$$

where the β's are the intercept and slope coefficients from equation (1), the $\gamma_{\bullet 0\text{'s}}$ are the mean intercept and slopes across trees, W_{1j} and W_{2j} are level 2 predictors (e.g., dbh), $\gamma_{\bullet 1}$ and $\gamma_{\bullet 2}$ are coefficients for W_{1j} and W_{2j}, and $u_{\cdot j}$ are random effects for tree *j*, which are assumed to be normally distributed with mean 0 and variance τ. Because it is assumed that the error terms in the HLM are normally distributed (Raudenbush and Bryk 2002), I visually inspected histograms of residuals to ensure data met this assumption.

I compared global models with correlated and uncorrelated random effects to determine which structure was more appropriate to the data. I selected the better supported model and used the same covariance structure for the remaining models. Analyses were conducted in Program R 2.11.0 (R Development Core Team 2010) and HLMs were executed with package lme4 (Bates and Maechler 2010).

I considered the level 1 variables ambient climate and number of bats to be nuisance variables because microclimate data was recorded for different trees under different ambient conditions and because metabolic heat could make comparisons between occupied and unoccupied trees problematic. Therefore, they were included to control for these factors when testing hypotheses relating tree structure to cavity microclimate. When modeling maximum cavity microclimate (i.e., temperature or relative humidity), the ambient climate predictors I considered were maximum ambient climate and the increase in ambient climate from the previous minimum to the current maximum. For minimum cavity microclimate, the predictors were minimum ambient climate and the decrease in ambient climate from the previous maximum to the current minimum. For cavity microclimate range, the predictors were the increase or decrease in ambient climate. Therefore, my initial model included ambient climate, change in ambient climate, and number of bats as level 1 fixed effects (X_{1ij}, X_{2ij}, and X_{3ij} in equation 1) and tree identity as a level 2 random effect on the intercept and slope ($u_{\cdot j}$ in equations 2, 3, 4, and 5).

There were no level 2 fixed effect predictors (i.e., $W_{\cdot j}$). In the terminology of Raudenbush and Bryk (2002), this was a random coefficients regression model.

To assess the effect of bat numbers on roost microclimate, I compared the initial HLMs to models that excluded the number of bats as a variable. These models were fit to data from 18 trees occupied on some days and not others to avoid confounding microclimate differences caused by bats with inherent microclimate differences between suitable and unsuitable trees. Only if the analysis indicated that the presence of bats did not impact roost microclimate, would further analyses compare microclimate data collected when bats were present to data collected when bats were absent. I compared evidence for models with and without the number of bat included and examined the predicted effect of bats on the microclimate to determine if bats impacted roost microclimate.

I also developed 7 to 10 HLMs to model the effect of ambient conditions on roost microclimate for each of the 6 microclimate variables. I used an exploratory approach in developing models instead of *a priori* hypothesis testing because I considered ambient climate conditions a nuisance variable. I used an information-theoretic approach (Burnham and Anderson 2002) to select the most parsimonious model relating ambient climate and roost microclimate. I used Akaike's Information Criteria (AIC; Akaike 1973) corrected for small sample bias (AIC_c; Hurvich and Tsai 1989) to assess evidence for the models, with the lowest AICc indicating the best supported model. The number of parameters used to estimate AICc included the fixed effects, random effects, error term, and random effect covariances when multiple random effects were included in the same candidate model (Burnham and Anderson 2002). I evaluated the relative strength of evidence for each model by calculating AIC weights (w_i; Burnham and Anderson 2002). I used this approach to select the most parsimonious models from sets of candidate models. I did not perform model averaging because it is not statistically appropriate for mixed models (Grueber et al. 2011).

After controlling for ambient climate and number of bats, I developed 17 models to weigh evidence for hypotheses relating tree structural characteristics to tree microclimate. I began with the best supported model relating ambient conditions to tree microclimate identified in the previous step. For each of 8 tree characters identified by my literature search, I created two models. One hypothesized that the character would only affect average microclimate conditions (W_{1j} in equation 2) and one hypothesized that the character would also affect the microclimate response to ambient conditions (W_{1j} in equations 3 and 4). In the terminology of Raudenbush and Bryk (2002), this was an intercepts and slopes as outcomes model. I also included a model with no tree structure variables for comparison. I defined the confidence set of models as models with weight ≥10% of top model weight. To evaluate the value of tree structure as a proxy for cavity microclimate, I report parameter estimates and standard errors for the level 2 coefficients.

I was also interested in the ability of each level of data (ambient climate at level 1 and tree structure at level 2) to explain the variation in cavity microclimate, so I partitioned the variance across levels to determine how much each level contributed to the error term and how much variance was resolved by each predictor variable. I calculated the intra-class correlation for each unconditional model and then calculated the percent reduction in variance after predictor variables were introduced at each level (Raudenbush and Bryk 2002).

In addition to microclimate differences among roosts, there may be differences within roosts (Lourenco and Palmeirim 2004). Additional literature review identified tree structures hypothesized to microclimate gradients within a tree, such as southern exposure (Table 4.1). I evaluated microclimate gradients in the 2 trees that received 5 data loggers each, using additional HLMs. I considered the effect of dummy variables for data logger position: height (elevated =1), cardinal direction (south = 1), wall contact (contact = 1) and tree identity (tree1 = 1). The models predicted cavity microclimate from ambient climate as level 1 fixed effects ($X._{ij}$ in equation 1), position within the cavity (e.g., height) as a level 2 fixed effect (W_{1j} in equations 2, 3, and 4), and data logger identity as level 2 random effects on intercept and slope ($u._{j}$ in equations 2, 3, and 4). I constructed eight models predicting roost microclimate from data logger position, plus a model with no data logger position variables for comparison. I used AICc weights to evaluate the relative strength of evidence for each model. To evaluate the value of tree structure as a proxy for cavity microclimate, I report parameter estimates and standard errors for the level 2 coefficients and the percent reduction in variance achieved by the best supported tree structure variable.

Effect of Microclimate on Bat Presence

Roost microclimate affects energy consumption in roosting bats (Speakman and Thomas 2003), although there are divergent hypotheses regarding exactly how this affects roost selection (Table 4.1). I weighed evidence for hypotheses relating microclimate characteristics of trees, assessed over the survey period, to the presence of bats at least once during the season. Therefore, any tree that was occupied at any time was considered occupied, while other trees were unoccupied. I related this bat presence to a “typical” microclimate in each tree, rather than hourly or daily microclimate data. Because the response variable was binary (bats present/absent) and there was only one typical microclimate per tree, I used ordinary logistic regression for the analysis (Hosmer and Lemeshow 2000). To quantify typical roost microclimate over the entire survey period, I used the Best Linear Unbiased Predictions (BLUPs) of random effects (Robinson 1991) from the best supported HLM model relating ambient climate to roost microclimate. The BLUP of the intercept predicts how much the microclimate of a tree differs from the population at average ambient conditions, while the BLUP of the slopes predict how much more or less the internal microclimate reacts to changes in ambient conditions. Therefore, I developed twelve models predicting bat presence from tree microclimate BLUPs, using the intercept or slope of each of the six microclimate characters as predictors. I also created a model predicting bat presence by tree volume because volume is known to affect Rafinesque's big-eared bat presence (Chapter 1) and an intercept-only model in which bat presence was random with respect to microclimate and volume, for comparison. I repeated the analysis for only maternity colonies of Rafinesque's big-eared bats because reproductive females may be more affected by roost microclimate due to the costs of reproduction (Racey and Swift 1981). I used AICc weights to evaluate the relative strength of evidence for each model.

I also examined the relationship between the microclimate characteristics of a tree on a particular day, and whether or not it was occupied on that same day using a hierarchical logistic model (HLogM; Wong and Mason 1985). The HLogMs differ from HLMs in that the response variable, bat presence or absence, is transformed via the logit link so that Y_{ij} in equation (1) is replaced by $\eta_{ij} = \ln(p_{ij}/(1-p_{ij}))$, where ln is the natural logarithm and p_{ij} is the probability of bat presence at time *i* in tree *j* (Wong and Mason 1985). The second difference is that there is no error term, e_{ij}, in the logistic model (Wong and Mason 1985). Again, I visually inspected histograms of residuals to determine if they were normally distributed.

The models predicted bat presence from tree microclimate as a level 1 fixed effect (X_{ij} in equation 1). The level 2 model allowed the effect of tree microclimate to vary with ambient conditions (W_{1j} and W_{2j} in equation 3) because a 25 °C roost might be considered warm or cool, depending on ambient conditions. Tree identity was included as a level 2 random effect on intercepts and slopes. Due to excess zeros (i.e., bat absence), models applied to the entire data set did not converge on stable estimates. Therefore, the daily analysis was limited to occupied trees and these models tested whether microclimate affected the days on which known roost trees were occupied; it did not distinguish between used and unused trees. I developed seven models predicting daily bat presence from tree microclimate, plus a model predicting bat presence by tree volume and a random effects ANOVA model (i.e., a model with no fixed effects) for comparison. I repeated the analysis for maternity colonies of Rafinesque's big-eared bats and I used AICc weights to evaluate the relative strength of evidence for each model.

RESULTS

I sampled 45 trees for a total of 284 days (mean = 6.3 days, range: 1-18 days). Due to malfunction of some humidity sensors, humidity was only sampled in 31 trees for a total of 195 days (mean = 6.3 days, range: 1-18 days). Occupied trees receiving data loggers were larger and more cavernous (dbh = 127 cm, cavity volume = 2,624 dm^3) than unoccupied trees receiving data loggers (dbh = 103 cm, cavity volume = 1,082 dm^3). Ambient conditions were generally warm and humid, while conditions inside cavities were buffered against external extremes (Figure 4.2). There were no obvious differences in means of microclimate variables between occupied and unoccupied trees, although occupied trees tended to lack rough interiors, have less canopy cover, and have larger volumes (Table 4.2). All global HLM models of cavity microclimate with correlated variances had lower AICc values than models with uncorrelated variances. Therefore, I used correlated variances for all models. Residuals of global HLMs did not differ by tree, indicating that the HLM accounted for much of the dependence in error terms within the trees (Figure 4.3A).

Factors Affecting Roost Microclimate

In assessing the effect of bats on roost temperature and humidity, removing bats from the global model improved model support for all six microclimate variables. The estimated impact of each bat on roost temperature was ≤0.01 °C and ≤0.05% relative humidity in all models. Therefore, I concluded that bats did not significantly impact measurements and I combined data collected when bats were present or absent for analysis.

The best supported model of maximum roost temperature was the most general model, which predicted maximum roost temperature from maximum ambient temperature and the increase in ambient temperature from the previous minimum to the current maximum, and allowed the ambient temperature effects to vary across hollow trees (Table 4.3; Appendix 4.A). This top model received 93.3% percent of the AICc weight and I concluded that this model would best account for the effect of the nuisance variable, ambient temperature. Therefore, I included these variables in all future models of maximum roost temperature. Comparisons of similar sets of models for the other 5 microclimate variables under consideration indicated that in every case the most general model was best supported and received >80% of the AICc weight (Table 4.3; Appendix 4.A). These top models of the effect of ambient conditions were the basis for all subsequent models of roost microclimate.

After controlling for ambient conditions, maximum temperature differed between measured trees by up to 5.80 °C (Figure 4.1A), minimum temperature differed by 7.70 °C, and temperature range by 8.48 °C. For humidity, the same differences between trees were 8.66%, 30.44%, and 23.69%, respectively. There was evidence that several tree structures affect cavity temperature, while cavity humidity was primarily affected by canopy cover (Table 4.4; Appendix

4.B). Some models in the confidence set indicated that tree characteristics shifted average microclimate (γ_{01} in equation 2), while others indicated a significant relationship between ambient conditions and microclimate (γ_{11} and γ_{21} in equations 3 and 4). All 6 microclimate variables were affected by ≥ 1 tree characteristics and all tree characteristics except dbh, solid wood volume, and rough walls affected some aspect of tree microclimate.

The intra-class correlation for maximum temperature indicated that approximately one half to three quarters of the variation in cavity microclimate could be attributed to differences among trees (Table 4.5). Ambient climate variables were generally able to explain >80% of the variation within individual trees. The one exception was maximum humidity, which was generally high, regardless of external conditions. In contrast, the best supported tree structure variables (from Table 4.4) explained less than 25% of the variation among trees.

Microclimate varied somewhat within trees (Figure 4.4). For example, in the afternoon, temperatures in measured locations in tree 1 differed by up to 1.1 °C, and humidity in tree 2 differed by up to 10.6%. Few models were better supported than the model with no tree variables (Table 4.6; Appendix 4.C). Both maximum temperature and humidity were best predicted by tree identity, with tree 1 being 0.75 °C warmer and tree 2 being 0.66% more humid. Minimum temperature was best predicted by southern exposure, with southern locations being 0.12 °C warmer. Tree structure variables were generally not helpful in predicting minimum humidity. Only 3.0% of variation in minimum cavity temperature was due to position within the tree. Including ambient temperature in the model accounted for 98.1% of the unexplained variance, while including southern exposure did not reduce the variance at all. Similarly, only `5.4% of variation in minimum cavity humidity was due to position in the tree. Ambient humidity accounted for 77.7% of the unexplained variance.

Effect of Microclimate on Bat Presence

The best supported logistic model of seasonal bat presence was the cavity volume model for all Rafinesque's big-eared bat colonies and for maternity colonies (Table 4.7). These top models received 99.2% and 75.9% of the AIC weight, respectively. For all colonies and maternity colonies, the intercept-only models were the second best models, and received more support than any models relating roost microclimate to colony presence.

Residuals of HLogMs differed by tree, indicating some dependence in error terms remained (Figure 4.3B).The best supported HlogM of daily bat presence was the maximum roost temperature model for all Rafinesque's big-eared bat colonies and for maternity colonies (Table 4.8). These top models received 74.1% and 95.7% of the AIC weight, respectively and were the only models with more support than the random effects ANOVA models. The top model for all colonies predicted that roosts were more likely to be occupied on days with an above average maximum cavity temperature, while the top model for maternity colonies made the opposite prediction (Table 4.9). However, the coefficient for maternity colonies had a wide confidence interval and the effect may not have differed from one. Both top models predicted that among roost trees, roosts were more likely to be occupied if they were more sensitive to maximum ambient temperature. The effect of large changes in ambient temperatures was ambiguous and may not have differed from one.

DISCUSSION

My results generally do not support the view that cavity microclimate is reliably related to tree structure, making it difficult to draw conclusions about roost microclimate from tree structure data. Furthermore, roost selection was not based on roost microclimate. Although warmer roosts were occupied on more days than cooler roosts, this result is limited by data quality. Given these results, it seems more likely that Rafinesque's big-eared bat selects tree roosts based on other criteria, such as avoiding predators.

Factors Affecting Roost Microclimate

Ambient conditions and tree structure affected roost microclimate, while the number of bats did not. In other studies where the presence of bats affected the recorded temperatures, either the cavity was much smaller than in my study (Willis and Brigham 2007) or the measuring device was placed closer to the roosting bats (Burnett and August 1981). Although the presence of bats did not affect measured microclimate in this study, there may have been a more localized effect that was not detected. Although the importance of ambient conditions on cavity microclimate has been established (Sedgeley 2001, Coombs et al. 2010), I found that both the level and change in ambient conditions affected microclimate. Most previous studies did not consider the effect of changes in ambient conditions (e.g., Vonhof and Barclay 1997, Willis and Brigham 2007). Based on my data, including the effect of changes in ambient conditions may improve model accuracy.

Although tree structure influenced microclimate, the most important tree characters in this study differed from common predictions. Dbh and canopy cover are most frequently hypothesized to affect cavity temperature (e.g., Brigham et al. 1997, Britzke et al. 2003), but those two factors were not among my best supported models of cavity temperature (Table 4.5). Dbh has the potential to affect cavity temperature through insulation provided by thick cavity walls, but hollow trees in my study frequently had cavity walls only a few cm thick encasing a cavity over 1 m wide. The thinner walls likely disrupted the usual relationship between dbh and insulation, resulting in no discernable relationship between dbh and microclimate. In addition, my study sites generally had high canopy cover and roosts close to the ground, which may have moderated solar radiation, while the study with the greatest predicted effect of tree structure occurred in burned clearcuts receiving maximal solar radiation (Vonhof and Barclay 1997).

Not only were the structures affecting microclimate different in my study, the effect size was relatively small, impacting maximum and minimum temperature by ≤ 2 °C. In contrast, the predicted effect of stump diameter on roost temperature was up to 15 °C in a study of western long-eared bats (*Myotis evotis*) in British Columbia (Vonhof and Barclay 1997). Among big brown bats (*Eptesicus fuscus*), the combined effect of tree species and health was 5 °C (Kalcounis and Brigham 1998). However, there was no effect of roost type (crevice or circular opening) or cavity volume on roost temperature in big brown bat tree roosts (Willis and Brigham 2007). Similarly, few tree structures had any effect on winter cavity temperature in a forest in central Ontario (Coombs et al. 2010). Given the variation in the tree structures most relevant to microclimate across studies, the range of effect sizes across studies, and the low percentage (<25) of variability explained in this study, it appears that tree structure is not a simple proxy for microclimate data and that tree structure data alone is inadequate for demonstrating that bats select roosts based on microclimate.

Cavities in artificial structures exposed to direct sunlight can achieve strong thermal gradients, allowing bats to select a microclimate by repositioning themselves (Licht and Leitner 1967, Lourenco and Palmeirim 2004). Large differences within tree cavities would enable bats to achieve optimal microclimate conditions by selecting a roost position, rather than a different roost. In contrast to studies in artificial structures, Willis and Brigham (2007) found that microclimate variability did not increase with tree cavity size in big brown bat tree roosts in Saskatchewan. Rafinesque’s big-eared bat roost trees in Louisiana with upper and lower entrances (as in my study), also showed no significant temperature differences between the upper and lower half of the roost (Rice 2009). The relatively small microclimate gradients in tree cavities may be due to greater canopy cover or different thermal properties of living trees. Regardless of the reason for the a lack of a gradient in tree cavities, my study along with other studies that have measured microclimate variability within trees suggest that bats roosting in tree cavities can only select their microclimate by tree selection or social behavior, but not by roost positioning.

Effect of Microclimate on Bat Presence

I found strong evidence that Rafinesque's big-eared bats select roosts with a large cavity volume and not roosts with an inherently different microclimate. It was more plausible that bats randomly selected roosts than that they selected roosts based on microclimate variables. In contrast, studies have concluded that temperature differences of < 5 °C play a role in tree roost selection (Kalcounis and Brigham 1998, Sedgeley 2001, Ruczynski 2006), as do humidity differences <8% (Sedgeley 2001). Cavity microclimate in my study varied by a greater amount, providing bats the opportunity to select roosts by microclimate, but they did not. The different result in my study suggests that ecological differences between this and other studies affect the basis for roost selection.

The irrelevance of microclimate to roost selection for Rafinesque's big-eared bats may be due to the particular species studied, ambient conditions, insect availability, or alternate selective pressures. The physiological response to microclimate varies between bat species (Webb et al. 1995, Speakman and Thomas 2003) so different roost selection criteria among bat species may be common. Other studies investigating microclimate in tree cavities have occurred at higher latitudes where ambient conditions are cooler with greater temperature fluctuations than in Georgia (Vonhof and Barclay 1997, Kalcounis and Brigham 1998, Sedgeley 2001, Ruczynksi

2006) which may elevate the importance of roost microclimate. Western long-eared bats at lower elevations select roost sites that are not as warm as bats at higher elevations (Solick and Barclay 2007) and perhaps lower latitude also frees Rafinesque's big-eared bats from selecting the warmest roosts. Warm roosts allow normothermic bats to consume less energy, reducing the need to forage (Speakman and Thomas 2003). During summer, sites in the Coastal Plain of Georgia have longer and warmer nights than higher latitude sites, which may yield greater insect abundance and reduce the cost of acquiring energy. Lower energetic costs for roosting may mean that other factors affecting roost selection, such as commuting costs, parasite loads, and threats from predators (Lewis 1995), assume a more important role for the population under study.

Even when roost occupancy is correlated with microclimate, results can be difficult to interpret because roost microclimate properties may vary with structural properties of trees (Vonhof and Barclay 1997). For example, occupied cavities are often elevated with little surrounding clutter (Kalcounis-Ruppell et al. 2005). These cavities may receive greater warmth from solar radiation, and therefore be more attractive to bats. Alternatively, elevated, uncluttered cavities may be attractive because they provide easier flight paths for bats, and warmer temperatures could be an irrelevant side effect. Thus, it can be difficult, absent experimentation, to determine which properties bats are selecting. Weighing the evidence for microclimate and structure simultaneously (Table 4.7) may help clarify the relative importance of the two factors. Overall, between entering torpor (Speakman and Thomas 2003), moving within roosts (Licht and Leitner 1967), and clustering behavior (Roverud and Chappell 1991), bats have substantial behavioral plasticity enabling them to deal with varied microclimate conditions without switching roosts. My results suggest that roost microclimate should be considered one plausible hypothesis, rather than the primary explanation of tree roost selection, until such a conclusion is better supported. Furthermore, the ultimate cause of roost selection may differ across habitats and bat species.

Although roost microclimate did not distinguish between used and unused cavities, it did help identify cavities occupied most frequently. However, results of the HLogM indicated observations were not independent, violating a model assumption (Figure 4.3B). This dependence may be because Rafinesque's big-eared bat typically roosts in one location for several consecutive days (Trousdale et al. 2008). Therefore, consecutive roost locations are not independent and much caution should be applied in interpreting the results.

If the result is not spurious, it suggests roost selection at two levels: bats determine which cavities are acceptable based on their volume, but then allocate their time between acceptable roosts based on microclimate. Roost occupancy has rarely been investigated on a daily basis, although big brown bats in Saskatchewan spend more days in tree cavities with larger volumes (Willis et al. 2006). It has been argued that some species select maternity roosts that are relatively warm at night, when females are apart from the young (Chruszcz and Barclay 2002). However, the result that daytime maximum temperature was most important provides more support for the idea that bats rely on passive warming in the afternoon to conserve energy as they prepare for evening emergence (Turbill 2006).

MANAGEMENT IMPLICATIONS

Tree structural characteristics, particularly cavity volume are more important to Ranfiesque's big-eared bat roost selection than cavity microclimate. In designing artificial roosts for this species, cavity size is likely to be most important, as long as microclimate is within the range observed here. Recommended targets are maximum temperature between 21 and 30 °C, minimum temperature between 14 and 26 °C, maximum humidity between 85 and 99%, and minimum humidity between 56 and 98%. Cavity microclimates outside this range were not evaluated and may or may not be suitable.

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Table 4.1: Hypotheses relating tree structure, roost microclimate, and bat presence; model variables; and references for summer roosts of Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) in the Coastal Plain of Georgia, 2008.

Hypotheses	**Model Variable**	**Example Reference**
Tree Structure Affects Roost Microclimate		
Wood properties	Tupelo	Boyles 2007
Air convection	Chimney	Rice 2009
Air convection	Holes	Ruczynski 2006
Solar Radiation	Canopy	Brigham et al. 1997
Tree health	Rough	Kalcounis and Brigham 1998
Insulation thickness	Dbh	Vonhof and Barclay 1997
Heat absorption	Trunk volume	Sedgeley 2001
Insulation/convection	Cavity volume	Sedgeley 2001
Random	None	None
Roost Position Affects Microclimate Gradient		
Solar radiation	South	Willis and Brigham 2005
Convection/insolation	Height	Ruczynski 2006
Conduction	Wall contact	Lausen and Barclay 2002
Random	None	None

Microclimate Affects Bat Use		
Diurnal passive rewarming	Max temperature	Turbill 2006
Nocturnal energy consumption of nonvolant pups	Min temperature	Lausen and Barclay 2003
Avoid temperature extremes	Temperature range	Wiebe 2001
Avoid nocturnal evaporative water loss by nonvolant pups	Max humidity	None found
Avoid diurnal evaporative water loss	Min humidity	Webb et al. 1995
Avoid humidity extremes	Humidity range	None found

Table 4.2: Mean and standard deviations (SD) of variables measured at trees occupied and unoccupied by Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) roost trees in the Coastal Plain of Georgia, 2008.

	Occupied (n=27)[1]		Unoccupied (n=18)[2]	
Variable	$\overline{X}$	SD	$\overline{X}$	SD
Temperature (°C)				
Roost Max	26.0	1.68	25.9	1.74
Roost Min	21.5	2.64	21.9	2.16
Range	4.48	2.28	3.96	2.46
Ambient Max	31.6	3.42	31.3	2.83
Ambient Min	20.4	2.94	20.8	2.83
Humidity (%)				
Roost Max	93.4	2.73	93.6	2.90
Roost Min	79.6	10.4	80.4	10.5
Range	13.8	8.62	13.2	8.27
Ambient Max	95.5	1.61	95.1	1.47
Ambient Min	65.4	13.1	61.9	11.5
Structure				
Tupelo (Y/N)	0.84	0.37	0.87	0.34
Chimney (Y/N)	0.39	0.49	0.38	0.49
Rough (Y/N)	0.07	0.25	0.30	0.46
Holes (#)	2.30	1.07	2.09	1.24
Canopy (%)	78.7	17.6	84.6	12.7
Cavity volume (*l*)	2,624	1,674	1,082	1,066
Trunk volume (*l*)	7,496	7,447	5,919	4,823
Dbh (cm)	126.8	29.0	102.9	37.4

[1] N=20 for humidity data
[2] N=12 for humidity data

Table 4.3: Best supported hierarchical linear models relating ambient conditions to tree cavity microclimate in hollow trees in the Coastal Plain of Georgia, 2008. Number of parameters in the model (K), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in AIC_c between a model and the model with the lowest AIC_c (ΔAIC_c), and model weights (w_i). Fixed effects refer to ambient conditions used as predictors and random effects refer to variables allowed to have tree-specific effects. See Appendix 4.A for additional models.

Model Name								
Level 1 fixed effects[a]		**Level 2 random effects**[b]						
X_1	X_2	u_0	u_1	u_2	**K**	**AICc**	**Δ AICc**	w_i
Maximum temperature								
Maximum	Increase	Trees	Trees	Trees	10	592.01	0.00	0.933
Minimum temperature								
Minimum	Decrease	Trees	Trees	Trees	10	375.28	0.00	1.000
Temperature range								
Increase		Trees	Trees		6	625.27	0.00	1.000
Maximum humidity								
Maximum	Increase	Trees	Trees	Trees	10	646.85	0.00	0.841
Minimum humidity								
Minimum	Decrease	Trees	Trees	Trees	10	1084.82	0.00	0.860
Humidity range								
Increase		Trees	Trees		6	1050.96	0.00	1.000

[a] see equation 1 in text.

[b] see equations 2, 3, 4 in text.

Table 4.4: Best supported hierarchical linear models relating tree characters and ambient conditions to tree cavity microclimate in hollow trees in the Coastal Plain of Georgia, 2008. Number of parameters in the model (K), difference in Akaike's Information Criterion adjusted for small sample size (AIC_c) between a model and the model with the lowest AIC_c (ΔAIC_c), model weights (w_i), estimated coefficients (β), and coefficient standard errors (SE). Models were an extension of models in Table 4.3. See Appendix 4.B for additional models.

***Model*/Level 2 Variable**	**K**	**Δ AICc**	**w_i**	**β**	**SE**
Max Temperature					
Chimney +	13	0.00	0.662	0.586	0.365
Chimney *Max +				0.241	0.044
Chimney *Increase				-0.068	0.042
Cavity volume +	13	3.14	0.137	0.014	0.158
Cavity *Max +				0.094	0.024
Cavity *Increase				-0.047	0.018
Min Temperature					
Holes volume +	13	0.00	0.294	-0.315	0.219
Holes *Min +				0.081	0.023
Holes *Decrease				0.014	0.010
Tupelo	11	0.41	0.240	1.177	0.472
Canopy	11	1.36	0.149	-0.026	0.012
Tupelo +	13	2.71	0.076	0.905	0.660
Tupelo *Min +				0.087	0.075
Tupelo *Decrease				-0.023	0.039
Temperature Range					
Holes +	8	0.00	0.650	0.731	0.224
Holes *Increase				0.063	0.030
Holes	7	2.13	0.224	0.286	0.076
Chimney +	8	4.42	0.071	1.697	0.576
Chimney*Increase				0.156	0.075

Max Humidity					
Canopy +	13	0.00	0.991	0.074	0.029
Canopy *Max +				-0.021	0.006
Canopy *Increase				0.002	0.001
Min Humidity					
Canopy +	13	0.00	1.000	0.017	0.117
Canopy *Min +				-0.038	0.008
Canopy *Decrease				0.030	0.007
Humidity Range					
Canopy +	8	0.00	0.762	0.083	0.095
Canopy *Increase				-0.008	0.003
Canopy	7	2.88	0.181	0.254	0.063

Table 4.5: Partition of variation in tree cavity microclimate. Percent of variation due to tree identity (intra-class correlation [ICC]), level 1 variables (i.e. ambient conditions) included in model, % of variation not due to tree ID (i.e., 1-ICC) accounted for by level 1 variables, level 2 variables (i.e., tree structure) included in model, and % of variation due to tree ID (ICC) accounted for by level 2 variables.

Tree cavity microclimate	**ICC**	**Level 1 variables**	**Level 1 variation explained**	**Level 2 variable**	**Level 2 variation explained**
Max Temp	50.7%	Max temp, Temp increase	86.9%	Chimney	11.4%
Min Temp	62.0%	Min temp, Temp decrease	97.2%	Holes	7.6%
Temp Range	76.0%	Temp increase	81.9%	Holes	21.9%
Max Humidity	73.6%	Max humid, Humid increase	67.4%	Canopy	24.9%
Min Humidity	58.8%	Min humid, Humid decrease	87.2%	Canopy	5.4%
Humid Range	50.5%	Humid increase	83.2%	Canopy	4.1%

Table 4.6: Best supported hierarchical linear models relating position in tree cavity and ambient climate to cavity microclimate in hollow trees in the Coastal Plain of Georgia, 2008. Number of parameters in the model (K), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in AIC_c between a model and the model with the lowest AIC_c (ΔAIC_c), and model weights (w_i), estimated coefficients (β), and coefficient standard errors (SE). Models were an extension of models in Table 4.3. See Appendix 4.C for additional models.

Model	**K**	**Δ AICc**	**w_i**	**β**	**SE**
Maximum Temperature					
Tree identity	11	0.00	0.705	0.746	0.174
Minimum Temperature					
South wall +	13	0.00	0.464	0.122	0.243
South*Min +				0.009	0.018
South*Decrease				-0.073	0.027
Maximum Humidity					
Tree identity +	13	0.00	0.817	-0.664	0.684
Tree*Min +				1.099	0.347
Tree*Decrease				-0.021	0.014
Minimum Humidity					
None	10	0.00	0.293	NA	NA

Table 4.7: Logistic regression models relating seasonal tree use by Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) to seasonal microclimate characters in the Coastal Plain of Georgia, 2008. Variables, number of parameters in the model (K), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in AIC_c between a model and the model with the lowest AIC_c (ΔAIC_c), and model weights (w_i).

Model	**K**	**AICc**	**Δ AICc**	$\mathbf{w_i}$
All Colonies				
Cavity volume	2	29.39	0.00	0.992
Null	1	42.46	13.08	0.001
Temperature range intercept	2	43.39	14.00	0.001
Minimum humidity intercept	2	43.54	14.16	0.001
Temperature range slope	2	43.56	14.17	0.001
Humidity range intercept	2	43.83	14.45	0.001
Maximum temperature intercept	2	44.02	14.64	0.001
Maximum humidity intercept	2	44.04	14.66	0.001
Minimum temperature intercept	2	44.34	14.95	0.001
Humidity range slope	2	44.56	15.18	0.000
Minimum humidity slope	3	45.72	16.33	0.000
Maximum humidity slope	3	46.25	16.86	0.000
Minimum temperature slope	3	46.33	16.95	0.000
Maximum temperature slope	3	46.46	17.08	0.000
Maternity Colonies				
Cavity volume	2	29.53	0.00	0.759
Null	1	35.26	5.73	0.043
Maximum humidity slope	3	35.42	5.89	0.040
Temperature range intercept	2	36.69	7.16	0.021
Temperature range slope	2	36.76	7.23	0.020

Maximum humidity intercept	2	36.92	7.39	0.019
Maximum temperature intercept	2	37.27	7.74	0.016
Minimum temperature intercept	2	37.35	7.82	0.015
Humidity range intercept	2	37.50	7.97	0.014
Humidity range slope	2	37.55	8.02	0.014
Minimum humidity intercept	2	37.55	8.02	0.014
Minimum temperature slope	3	37.95	8.43	0.011
Maximum temperature slope	3	38.33	8.80	0.009
Minimum humidity slope	3	39.95	10.43	0.004

Table 4.8: Hierarchical logistic regression models relating daily tree use to daily microclimate characters in occupied roost trees, for Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) in the Coastal Plain of Georgia, 2008. Variables, number of parameters in the model (K), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in AIC_c between a model and the model with the lowest AIC_c (ΔAIC_c), and model weights (w_i).

Model	**K**	**AICc**	**Δ AICc**	**w_i**
All Colonies				
Maximum temperature	7	166.44	0.00	0.741
Random effects ANOVA	2	170.36	3.92	0.104
Cavity volume	3	170.72	4.28	0.087
Minimum temperature	7	172.43	5.99	0.037
Temperature range	6	173.50	7.06	0.022
Maximum humidity	7	176.90	10.47	0.004
Minimum humidity	7	177.58	11.15	0.003
Humidity range	6	177.68	11.24	0.003
Maternity Colonies				
Maximum temperature	7	45.43	0.00	0.957
Random effects ANOVA	2	52.63	7.20	0.026
Cavity volume	3	54.33	8.90	0.011
Temperature range	6	55.79	10.36	0.001
Humidity range	6	60.67	15.24	0.000
Minimum temperature	7	63.57	18.14	0.000
Minimum humidity	7	64.16	18.73	0.000
Maximum humidity	7	64.34	18.91	0.000

Table 4.9: Estimates (coefficients for fixed effects and variance for random effects), odds ratios, and odds ratio confidence limits for the confidence set of hierarchical logistic models relating daily microclimate conditions to daily presence of Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) in the Coastal Plain of Georgia, 2008.

				90% Confidence Interval	
Parameters	**Estimate**	**SE**	**Odds Ratio**	**Lower**	**Upper**
Maximum temperature – All Colonies					
Fixed Effects					
Intercept	-1.035	0.441			
Max tree temp	0.348	0.170	1.417	1.070	1.876
Max tree temp*Max ambient temp	0.129	0.056	1.137	1.037	1.247
Max tree temp*Increase ambient temp	-0.086	0.058	0.918	0.833	1.01
Random Effects					
Intercept	2.041	1.429			
Max tree temp	0.088	0.297			
Max temperature – Maternity Colonies					
Fixed Effects					
Intercept	-5.159	2.142			
Max tree temp	-2.030	1.934	0.131	0.005	3.194
Max tree temp*Max ambient temp	0.336	0.151	1.399	1.091	1.794
Max tree temp*Increase ambient temp	0.069	0.150	1.071	0.836	1.372
Random Effects					
Intercept	12.368	3.517			
Max tree temp	12.234	3.498			

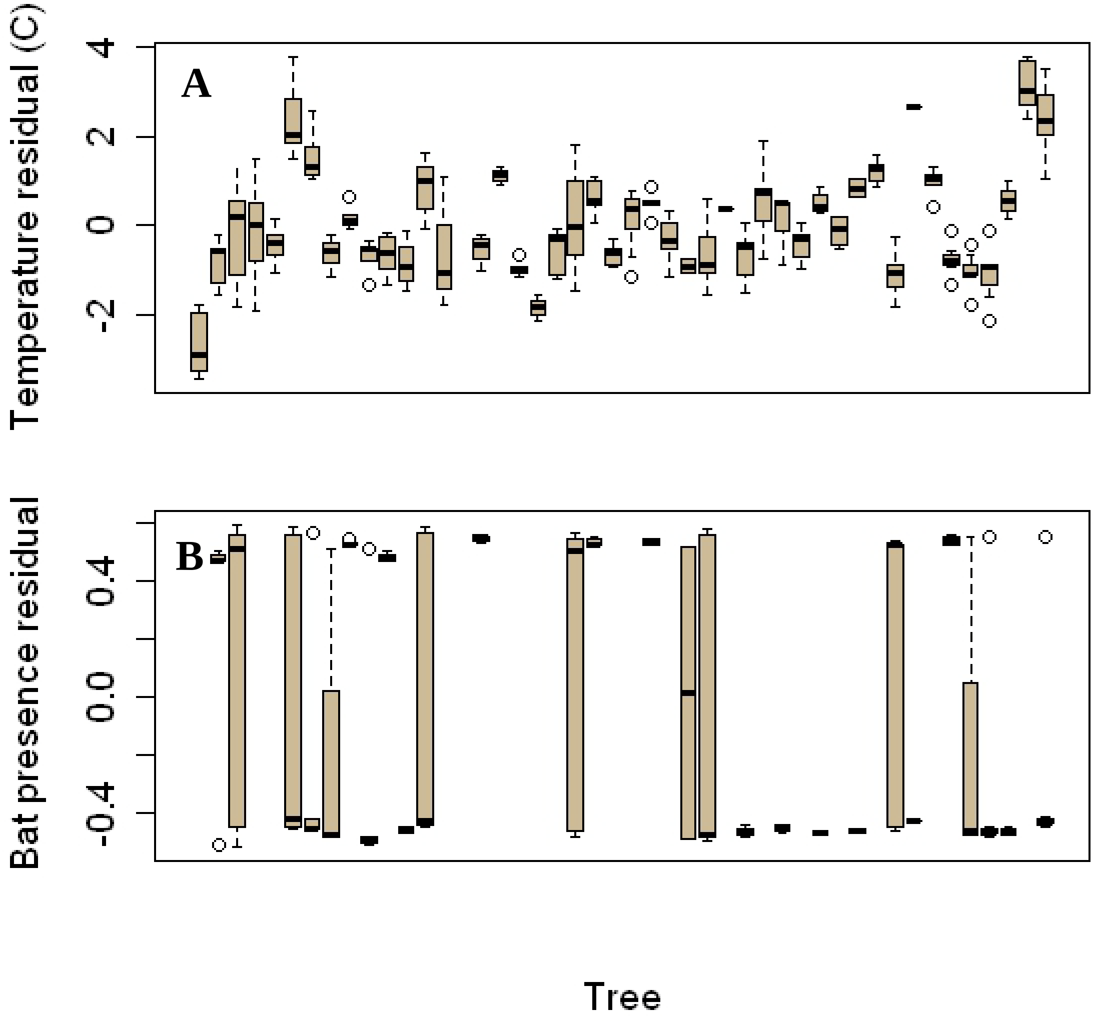

Figure 4.1: Residuals A) from linear regression model predicting maximum temperature in tree cavities from ambient temperature and B) from logistic regression model predicting bat presence in tree cavities from microclimate, using data collected in the Coastal Plain of Georgia, USA, 2008.

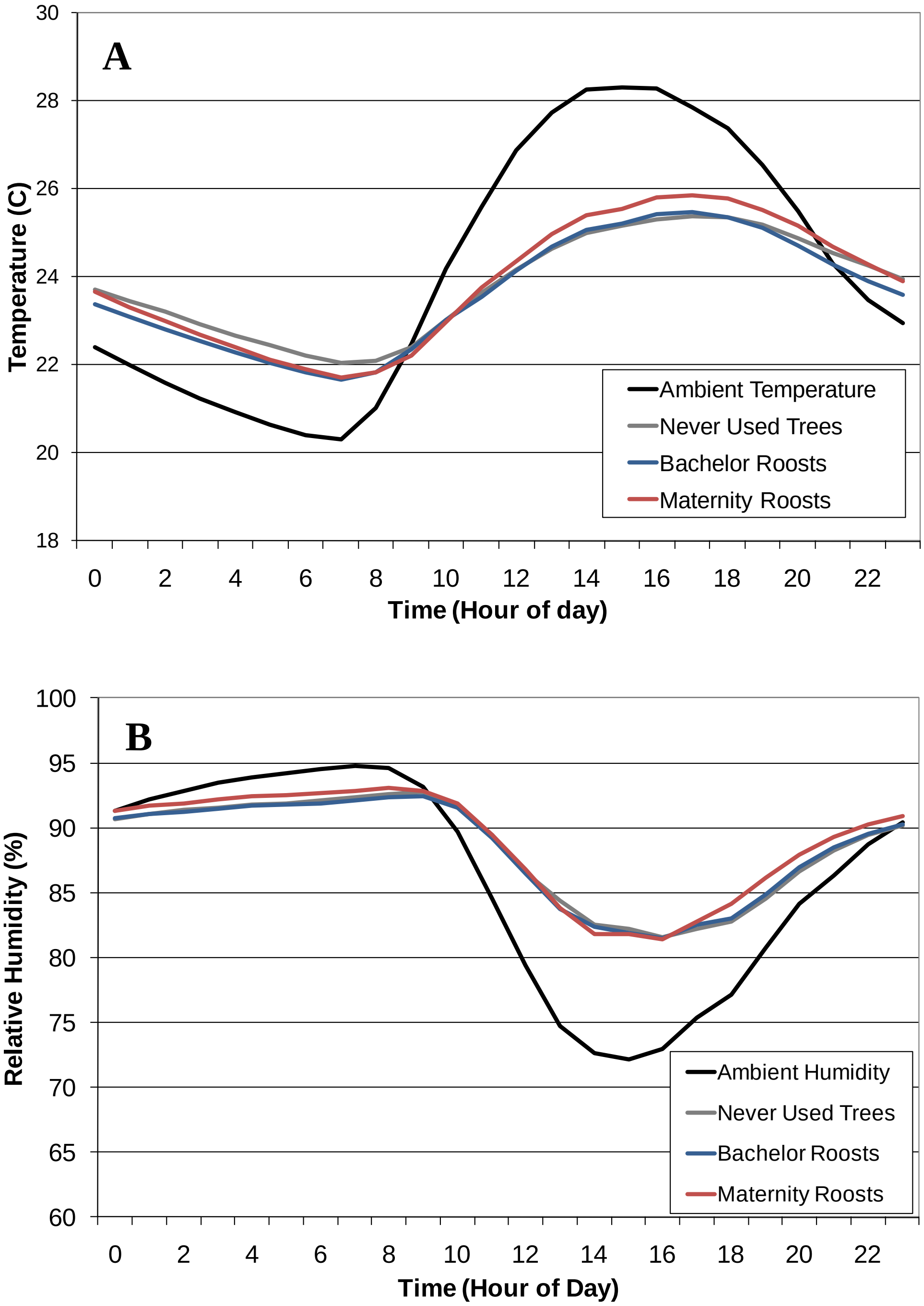

Figure 4.2: Average hourly temperature and humidity recorded in occupied and unoccupied tree cavities and ambient temperatures from May 21 to August 16, 2008 in the Coastal Plain of Georgia, USA.

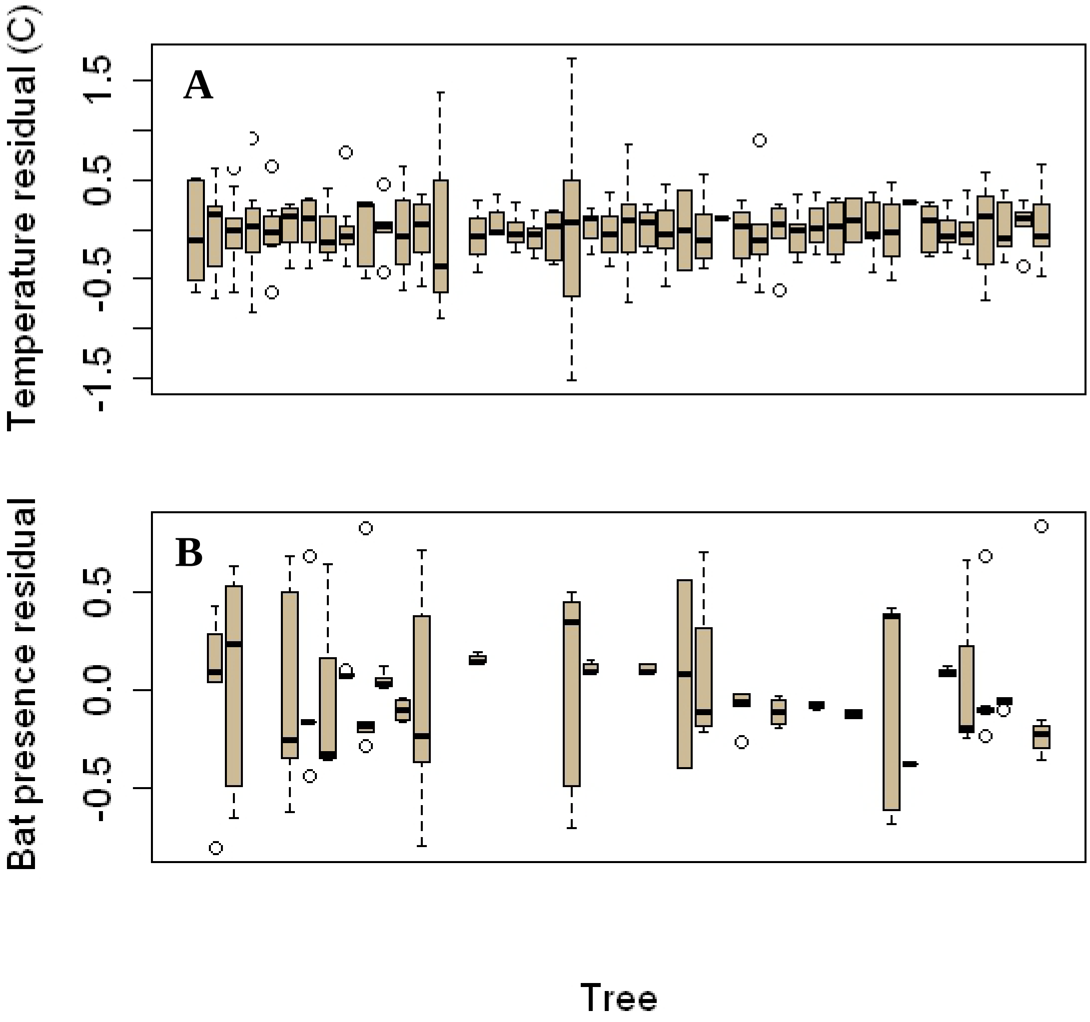

Figure 4.3: Residuals A) from hierarchical linear regression model predicting maximum temperature in tree cavities from ambient temperature and B) from hierarchical logistic regression model predicting bat presence in tree cavities from microclimate, using data collected in the Coastal Plain of Georgia, USA, 2008.

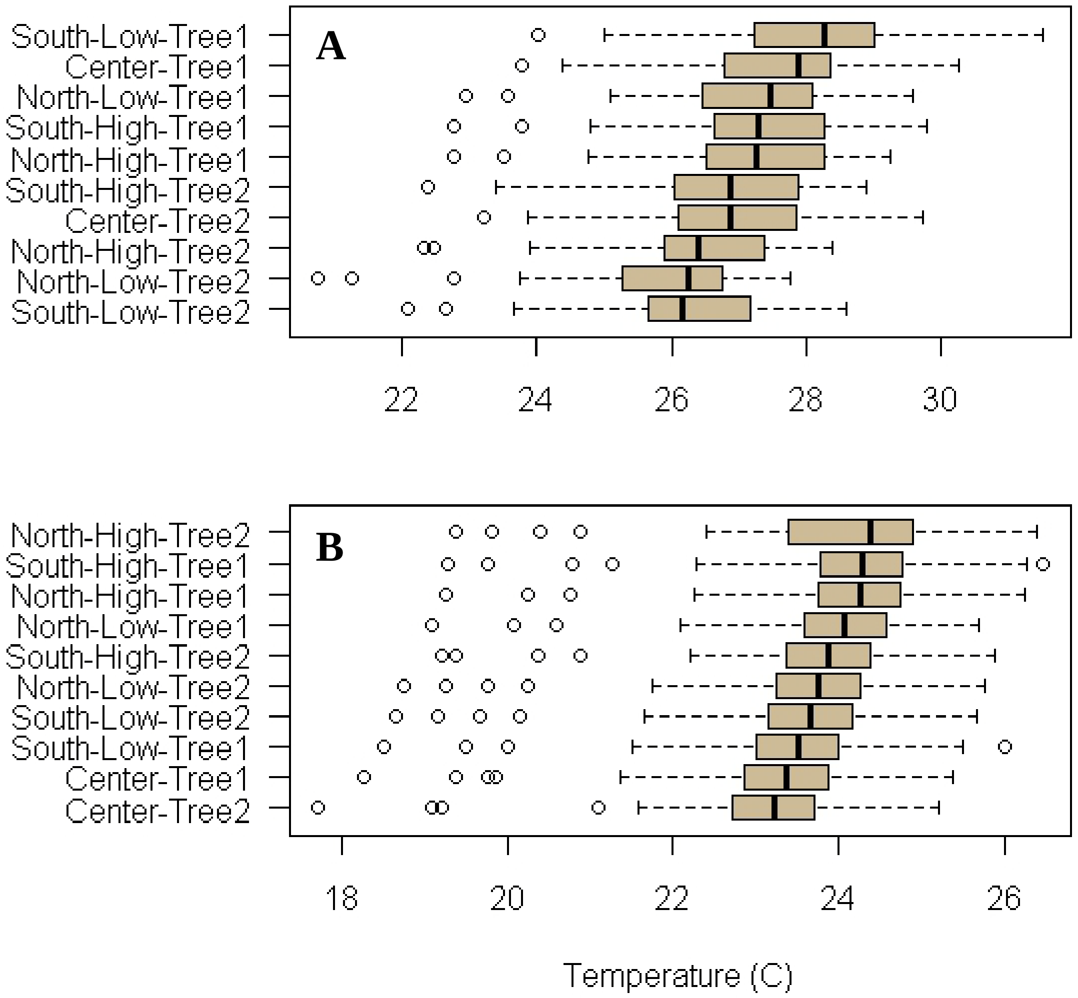

Figure 4.4: Temperature variation by location within a tree cavity for A) maximum temperature and B) minimum temperature for 2 hollow water tupelo in the Coastal Plain of Georgia, USA, 2008.

Appendix 4.A. Hierarchical linear models relating ambient conditions to tree cavity microclimate in hollow trees in the Coastal Plain of Georgia, 2008. Number of parameters in the model (K), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in AIC_c between a model and the model with the lowest AIC_c (ΔAIC_c), and model weights (w_i). Fixed effects refer to ambient conditions used as predictors and random effects refer to variables allowed to have tree-specific effects.

Model Name								
Level 1 fixed effects[a]		**Level 2 random effects**[b]						
X_1	**X_2**	**u_0**	**u_1**	**u_2**	**K**	**AICc**	**Δ AICc**	**w_i**
Maximum temperature								
Maximum	Increase	Trees	Trees	Trees	10	592.01	0.00	0.933
Maximum	Increase	Trees	Trees		7	584.17	4.91	0.079
Maximum	Increase	Trees		Trees	7	602.94	23.69	0.000
Maximum	Increase	Trees			5	648.45	69.20	0.000
Maximum		Trees	Trees		6	714.85	135.60	0.000
Maximum		Trees			4	781.36	202.11	0.000
Maximum	Increase		Trees	Trees	7	813.24	233.98	0.000
Maximum	Increase		Trees		5	866.20	286.94	0.000
Maximum	Increase			Trees	5	874.79	295.53	0.000
		Trees			3	1004.48	425.23	0.000
Minimum temperature								
Minimum	Decrease	Trees	Trees	Trees	10	375.28	0.00	1.000
Minimum	Decrease	Trees	Trees		7	392.99	17.71	0.000
Minimum		Trees	Trees		6	456.52	81.24	0.000

Minimum	Decrease	Trees		Trees	7	458.10	82.81	0.000
Minimum	Decrease	Trees			5	576.97	201.69	0.000
Minimum		Trees			4	630.39	255.11	0.000
Minimum	Decrease		Trees	Trees	7	1054.69	679.41	0.000
Minimum	Decrease		Trees		5	1084.08	708.80	0.000
Minimum	Decrease			Trees	5	1111.24	735.96	0.000
		Trees			3	1148.10	772.82	0.000
Temperature range								
Increase		Trees	Trees		6	625.27	0.00	1.000
Increase		Trees			4	806.56	181.29	0.000
	Decrease	Trees		Trees	6	905.09	279.82	0.000
	Decrease	Trees			4	933.85	308.58	0.000
		Trees			3	1017.66	392.39	0.000
Increase			Trees		4	1182.74	557.47	0.000
	Decrease			Trees	4	1223.28	598.01	0.000
Maximum humidity								
Maximum	Increase	Trees	Trees	Trees	10	646.85	0.00	0.841
Maximum	Increase	Trees	Trees		7	650.34	3.49	0.147
Maximum		Trees	Trees		6	655.57	8.72	0.011
Maximum	Increase	Trees		Trees	7	660.05	13.20	0.001
Maximum	Increase	Trees			5	684.43	37.58	0.000
Maximum		Trees			4	690.42	43.57	0.000
		Trees			3	796.91	150.05	0.000
Maximum	Increase			Trees	5	870.41	223.56	0.000

Maximum	Increase		Trees	Trees	7	874.70	227.84	0.000
Maximum	Increase		Trees		5	885.11	238.26	0.000
Minimum humidity								
Minimum	Decrease	Trees	Trees	Trees	10	1084.82	0.00	0.860
Minimum	Decrease	Trees	Trees		7	1088.69	3.88	0.124
Minimum		Trees	Trees		6	1092.82	8.00	0.016
Minimum	Decrease	Trees		Trees	7	1110.21	25.40	0.000
Minimum		Trees			4	1164.33	79.52	0.000
Minimum	Decrease	Trees			5	1166.35	81.53	0.000
		Trees			3	1365.32	280.51	0.000
Minimum	Decrease		Trees		5	1366.08	281.27	0.000
Minimum	Decrease			Trees	5	1366.08	281.27	0.000
Minimum	Decrease		Trees	Trees	7	1370.37	285.56	0.000
Humidity range								
Increase		Trees	Trees		6	1050.96	0.00	1.000
	Decrease	Trees		Trees	6	1107.75	56.79	0.000
Increase		Trees			4	1112.04	61.09	0.000
	Decrease	Trees			4	1138.00	87.04	0.000
	Decrease			Trees	4	1297.52	246.56	0.000
Increase			Trees		4	1299.56	248.60	0.000
		Trees			3	1306.13	255.17	0.000

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[a] see equation 1 in text.

[b] see equations 2, 3, 4 in text.

Appendix 4.B. Hierarchical linear models relating tree characters and ambient conditions to tree cavity microclimate in hollow trees in the Coastal Plain of Georgia, 2008. Number of parameters in the model (K), difference in Akaike's Information Criterion adjusted for small sample size (AIC_c) between a model and the model with the lowest AIC_c (ΔAIC_c), and model weights (w_i).

Model	**K**	**AICc**	**Δ AICc**	**w_i**
Maximum Temperature				
Chimney + Chimney*Ambient	13	569.64	0.00	0.662
Cavity volume + Cavity*Ambient	13	572.79	3.14	0.137
Holes	11	574.42	4.77	0.061
Holes + Holes*Ambient	13	574.53	4.89	0.057
Trunk volume	11	576.07	6.43	0.027
Canopy	11	576.29	6.65	0.024
None	10	579.26	9.61	0.005
Tupelo	11	579.54	9.90	0.005
Canopy + Canopy*Ambient	13	579.61	9.97	0.005
Dbh	11	579.65	10.01	0.004
Trunk volume + Trunk*Ambient	13	580.21	10.57	0.003
Chimney	11	580.85	11.21	0.002
Rough	11	580.96	11.32	0.002
Cavity volume	11	581.33	11.69	0.002
Tupelo + Tupelo*Ambient	13	582.20	12.56	0.001
Dbh + Dbh*Ambient	13	583.06	13.42	0.001
Rough + Rough*Ambient	13	583.60	13.96	0.001
Minimum Temperature				
Holes + Holes*Ambient	13	371.48	0.00	0.294
Tupelo	11	371.90	0.41	0.240
Canopy	11	372.85	1.36	0.149
Tupelo + Tupelo*Ambient	13	374.19	2.71	0.076

None	10	375.28	3.80	0.044
Cavity volume + Cavity*Ambient	13	376.13	4.65	0.029
Canopy + Canopy*Ambient	13	376.22	4.73	0.028
Dbh	11	376.57	5.08	0.023
Rough	11	376.87	5.38	0.020
Chimney + Chimney*Ambient	13	376.87	5.39	0.020
Holes	11	377.18	5.70	0.017
Trunk volume	11	377.25	5.76	0.016
Chimney	11	377.27	5.79	0.016
Cavity volume	11	377.44	5.95	0.015
Dbh + Dbh*Ambient	13	378.95	7.47	0.007
Rough + Rough*Ambient	13	380.34	8.85	0.004
Trunk volume + Trunk*Ambient	13	380.68	9.20	0.003
Temperature Range				
Holes + Holes*Ambient	8	615.51	0.00	0.650
Holes	7	617.64	2.13	0.224
Chimney + Chimney*Ambient	8	619.93	4.42	0.071
Chimney	7	621.85	6.34	0.027
None	6	625.27	9.76	0.005
Cavity volume	7	625.66	10.15	0.004
Trunk volume	7	626.13	10.62	0.003
Cavity volume + Cavity*Ambient	8	626.45	10.94	0.003
Canopy	7	626.81	11.30	0.002
Rough	7	627.08	11.57	0.002
Tupelo	7	627.24	11.73	0.002
Dbh	7	627.25	11.74	0.002
Trunk volume + Trunk*Ambient	8	628.21	12.70	0.001
Canopy + Canopy*Ambient	8	628.40	12.89	0.001
Dbh + Dbh*Ambient	8	628.81	13.30	0.001
Tupelo + Tupelo*Ambient	8	628.98	13.47	0.001
Rough + Rough*Ambient	8	629.18	13.67	0.001

Maximum Humidity				
Canopy + Canopy*Ambient	13	631.84	0.00	0.991
Trunk volume	11	643.68	11.85	0.003
Trunk volume + Trunk*Ambient	13	644.78	12.94	0.002
Holes	11	646.46	14.62	0.001
Tupelo	11	646.48	14.64	0.001
Dbh + Dbh*Ambient	13	646.50	14.67	0.001
None	10	646.85	15.02	0.001
Cavity volume	11	647.18	15.34	0.000
Holes + Holes*Ambient	13	647.53	15.69	0.000
Dbh	11	647.76	15.93	0.000
Rough	11	647.90	16.07	0.000
Canopy	11	647.91	16.08	0.000
Chimney	11	648.29	16.46	0.000
Cavity volume + Cavity*Ambient	13	649.06	17.22	0.000
Tupelo + Tupelo*Ambient	13	649.28	17.45	0.000
Rough + Rough*Ambient	13	650.69	18.85	0.000
Chimney + Chimney*Ambient	13	651.46	19.62	0.000
Minimum Humidity				
Canopy + Canopy*Ambient	13	1063.23	0.00	1.000
Canopy	11	1080.94	17.70	0.000
Chimney	11	1082.43	19.19	0.000
Holes	11	1084.46	21.22	0.000
Cavity volume	11	1084.50	21.27	0.000
Dbh + Dbh*Ambient	13	1084.58	21.35	0.000
None	10	1084.82	21.58	0.000
Chimney + Chimney*Ambient	13	1085.38	22.14	0.000
Cavity volume + Cavity*Ambient	13	1085.90	22.66	0.000
Dbh	11	1086.11	22.88	0.000
Trunk volume + Trunk*Ambient	13	1086.16	22.93	0.000
Rough	11	1086.44	23.21	0.000

Trunk volume	11	1086.55	23.31	0.000
Tupelo	11	1087.04	23.80	0.000
Holes + Holes*Ambient	13	1088.77	25.53	0.000
Rough + Rough*Ambient	13	1090.25	27.02	0.000
Tupelo + Tupelo*Ambient	13	1090.97	27.74	0.000
Humidity Range				
Canopy + Canopy*Ambient	8	1038.19	0.00	0.762
Canopy	7	1041.06	2.88	0.181
Chimney	7	1044.52	6.33	0.032
Chimney + Chimney*Ambient	8	1046.57	8.38	0.012
Dbh + Dbh*Ambient	8	1049.46	11.27	0.003
Cavity volume	7	1050.38	12.19	0.002
Cavity volume + Cavity*Ambient	8	1050.54	12.35	0.002
Holes	7	1050.67	12.49	0.001
None	6	1050.96	12.77	0.001
Trunk volume + Trunk*Ambient	8	1051.04	12.85	0.001
Dbh	7	1052.19	14.00	0.001
Rough	7	1052.36	14.17	0.001
Holes + Holes*Ambient	8	1052.77	14.59	0.001
Trunk volume	7	1052.81	14.62	0.001
Tupelo	7	1052.95	14.76	0.000
Rough + Rough*Ambient	8	1054.51	16.32	0.000
Tupelo + Tupelo*Ambient	8	1054.77	16.58	0.000

Appendix 4.C. Hierarchical linear models relating position in tree cavity and ambient climate to cavity microclimate in hollow trees in the Coastal Plain of Georgia, 2008. Number of parameters in the model (K), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in AIC_c between a model and the model with the lowest AIC_c (ΔAIC_c), and model weights (w_i).

Model	**K**	**AICc**	**Δ AICc**	$\mathbf{w_i}$
Maximum Temperature				
Tree identity (ID)	11	999.59	0.00	0.705
Tree ID + ID*ambient	13	1001.66	2.07	0.250
No fixed effects	10	1007.01	7.42	0.017
Center	11	1008.64	9.06	0.008
Raised 3.5 m	11	1008.99	9.40	0.006
South wall	11	1009.01	9.42	0.006
Cavity wall + wall*ambient	13	1009.37	9.78	0.005
South wall + south*ambient	13	1011.82	12.24	0.002
Raised 3.5 m + raised*ambient	13	1012.84	13.25	0.001
Minimum Temperature				
South wall + south*ambient	13	8.43	0.00	0.464
Raised 3.5 m + raised*ambient	13	9.02	0.59	0.346
South wall	11	11.71	3.28	0.090
Cavity wall + wall*ambient	13	12.87	4.44	0.051
Raised 3.5 m	11	14.53	6.09	0.022
No fixed effects	10	16.07	7.64	0.010
Cavity wall	11	16.45	8.01	0.008
Tree ID	11	17.00	8.56	0.006
Tree ID + ID*ambient	13	19.50	11.07	0.002
Maximum Humidity				
Tree ID + ID*ambient	13	979.10	0.00	0.817
Tree ID	11	982.48	3.39	0.150

Raised 3.5 m + raised*ambient	13	987.95	8.85	0.010
No fixed effects	10	988.42	9.33	0.008
Raised 3.5 m	11	988.95	9.85	0.006
South wall	11	990.05	10.96	0.003
Cavity wall	11	990.35	11.25	0.003
South wall + south*ambient	13	991.47	12.38	0.002
Cavity wall + cavity*ambient	13	992.59	13.49	0.001
Minimum Humidity				
No fixed effects	10	2115.83	0.00	0.293
South wall	11	2117.00	1.16	0.163
Cavity wall + cavity*ambient	13	2117.32	1.48	0.140
Raised 3.5 m	11	2117.79	1.95	0.110
Tree ID	11	2117.82	1.99	0.108
Cavity wall	11	2117.84	2.01	0.107
Tree ID + ID*ambient	13	2120.03	4.19	0.036
South wall + south*ambient	13	2120.55	4.72	0.028
Raised 3.5 m + raised*ambient	13	2121.76	5.93	0.015

CHAPTER 5

PREDICTIVE DENSITY MODEL FOR TREE ROOSTING COLONIES OF RAFINESQUE'S BIG-EARED BAT[4]

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[4] Clement, M. J. and S. B. Castleberry. To be submitted to the *Journal of Mammalogy*.

ABSTRACT

Data on species distribution and abundance are the foundation of science-based wildlife management. However, due to difficulties in surveying bats, abundance estimates are rare, especially for tree-roosting microchiropterans. Therefore, my objective was to develop a geographic habitat-abundance model for Rafinesque's big-eared bat to generate predictive maps and estimate colony abundance and density. I used transect searches at 8 study sites in the Coastal Plain of Georgia, USA to locate and characterize Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) diurnal summer roosts. I searched 123 transects during 2007 and 2008 and found 41 transects were occupied by 179 colonies holding 512 bats. I modeled the relationship between the number of bat colonies and landscape scale habitat variables with zero-inflated negative binomial regression and used Akaike's information criterion and Akaike weights to select the most parsimonious models. I generated a predictive density map to identify areas of high colony density and to estimate overall abundance. Colony density was predicted by the duration of wetland flooding, wetland width, and study site. I estimated there were 2,190 colonies containing 6,032 bats in trees with basal hollows on the 8 study sites. Predicted density ranged from 0.04 colonies/ha and 0.04 bats/ha in saturated wetlands to 0.27 colonies/ha and 1.15 bats/ha in semi-permanently flooded wetlands. Across study sites, density varied from 0.08 colonies/ha and 0.16 bats/ha to 0.21 colonies/ha and 0.66 bats/ha. My results can be used to identify potential habitat for Rafinesque's big-eared bat from GIS data, estimate abundance, and assess species status and evaluate management activities.

INTRODUCTION

Successful wildlife management requires reliable data on species distribution and abundance (Sinclair et al. 2006). Identifying goals, documenting impacts, and recognizing successes of management are possible when changes in distribution and abundance can be assessed. Predictive mapping of landscape scale habitat associations can be used to assess species status, locate areas of ecological importance, and support conservation planning and management (Guisan and Thuiller 2005). However, identifying habitat associations and abundance of forest dwelling bats has proven particularly difficult (Carter et al. 2003, Kunz et al. 2009).

While studies have developed predictive geographic models of bat presence (Jaberg and Guisan 2001, Greaves et al. 2006, Watrous et al. 2006, Duff and Morrell 2007, Rebelo and Jones 2010), predictive models estimating bat density have not been developed, primarily due to the difficulty in estimating abundance While many types of observations can be used in presence models, abundance estimates require counts of bats, estimates of detection probability, and area surveyed (Williams et al. 2002). Under ideal conditions, estimates of these parameters for cave roosting bats may be tractable, enabling abundance estimates (Tuttle 2003, Hayes et al. 2009). However, for tree-roosting species, there are few methods for estimating detection probabilities or area occupied. Acoustic surveys cannot identify individual bats and therefore cannot be a basis for abundance estimates (Hayes 2000). Mist net or harp trap surveys do not yield reliable abundance estimates (Weller 2007). Locating roosts through radio-telemetry, a common focus of bat research, leaves many roosts undiscovered, making abundance estimates impossible (Willis et al. 2006). Assumptions of mark-recapture models are unlikely to be met when mist-netting forest bats (Kunz et al. 2009). Even if detection probability and total population were known, the area containing bats would be unknown (Weller 2007).

As an alternative, repeated roost surveys within an area could, theoretically, generate counts of bats, detection probabilities, and a known area. However, because tree roosts are typically well-hidden, roost searches for tree cavity-roosting microchiroptera have rarely been attempted (but see Sedgeley and O'Donnell 1999, Stevenson 2008, Rice 2009). Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) is a small, insectivorous bat restricted to the southeastern United States (Jones 1977). In the Coastal Plain, it is most commonly associated with bottomland hardwood forests and cypress (*Taxodium*)-gum (*Nyssa*) swamps (Clark 2003) where it roosts in hollow trees (Harvey et al. 1999). Roost trees typically have basal hollows, making the roosts and occupants relatively conspicuous (Carver and Ashley 2008). The accessible roosts make repeated roost surveys feasible, enabling density estimates, which, combined with habitat data, could be the basis for a geographic model of bat density. Therefore, my objectives were to 1) develop a fine-scale habitat-abundance model for Rafinesque's big-eared bat incorporating roost surveys, habitat data, and geographic information systems (GIS) to generate predictive maps and 2) estimate colony abundance and density on selected study sites.

METHODS

Study Area

I collected data at 8 sites in the Coastal Plain of Georgia, USA. All study sites were state-managed and located within a major river floodplain with cypress-gum swamps and bottomland hardwoods as major habitat components. I conducted field work in Moody Forest Natural Area, Ocmulgee Wildlife Management Area (WMA), and Tuckahoe WMA from May 11 to August 14, 2007 and in Beaverdam WMA, Chickasawhatchee WMA, Clayhole Swamp WMA, Little Satilla WMA, and River Bend WMA from May 13 to August 16, 2008. Sites were selected to achieve wide distribution across the Georgia Coastal Plain and to ensure inclusion of sites with forested cypress-gum swamp habitat across a range of ages. Major river systems influencing study sites included the Altamaha, Flint, Little Satilla, Ocmulgee, Oconee, and

Savannah rivers (Figure 5.1). Study areas ranged from 1,416 ha (River Bend WMA) to 8,597 ha (Ocmulgee WMA) with area in cypress-gum swamp habitat ranging from 535 ha (Moody Forest Natural Area) to 2,178 ha (Chickasawhatchee WMA).

Transect Searches

I searched for Rafinesque's big-eared bat colonies from May 11 to August 14, 2007 and May 13 to August 16, 2008. I stratified the study areas by habitat type using wetland categories defined by the US Fish and Wildlife Service's National Wetland Inventory (NWI; Cowardin et al. 1979). Given that Rafinesque's big-eared bats are found in hydric forest types (Clark 2003), I selected 3 habitat types in palustrine, forested wetland categories: saturated, seasonally flooded, and semi-permanently flooded. Saturated wetlands have saturated soil for extended periods, but surface water is rare. Seasonally flooded wetlands have surface water for extended periods early in the growing season, but no surface water late in the growing season. Semi-permanently flooded wetlands have surface water during the entire growing season in most years.

I created 500 m long linear transects along the approximate center of all wetland areas using ArcMap (version 9.2, ESRI Inc., Redlands, CA). I randomly selected transects to survey at each site from each wetland category. I over-sampled semi-permanently flooded wetlands relative to available area because Rafinesque's big-eared bats roost near water (Lance et al. 2001, Gooding and Langford 2004) in hydrophilic tree species (Trousdale and Beckett 2005, Carver and Ashley 2008). In 2007, forested wetlands on the study sites were 63% saturated, 27% seasonally flooded, and 10% semi-permanently flooded and I selected approximately 1/3 of transects from each habitat type (Table 5.1). In 2008, both transects and habitat were more heavily weighted towards semi-permanently flooded habitat, with 8% of transects in saturated, 25% in seasonally flooded, and 67% in semi-permanently flooded habitat. Across the study areas, forested wetland areas consisted of 23% was saturated, 41% seasonally flooded, and 36% semi-permanently flooded wetlands.

I walked the center of each transect and searched for trees with basal hollows within 15 m of the transect. Each transect was searched 3 times during the summer. Hollow trees were marked with flagging and visually inspected for bats using a spotlight and mirror. It was only possible to search a tree if the opening was at least 3 cm by 15 cm and no more than 1.8 m above the ground. I estimated the number of bats inside each occupied tree by counting visible bats. I classified colonies with <3 bats as bachelor colonies and colonies with ≥3 bats as maternity colonies because solitary bats are typically adult males (Trousdale and Beckett 2004) and adult males rarely join maternity colonies (England et al 1990). Additionally, maternity colonies were confirmed by the presence of juvenile bats, identifiable by their darker pelage (Jones 1977). On the rare occasions I observed exactly two bats in a roost, neither had juvenile pelage, so I recorded them as males.

Model Development and Analysis

The response variable in my analysis was total number of colonies on a transect after 3 surveys. A bat colony is sometimes defined as a social unit that may occupy multiple roosts (Kunz et al. 2009), but it is difficult to establish social relatedness of unmarked bats and irrelevant to abundance estimates. Therefore, I defined a bat colony as a group of bats in a single roost at the time of observation. Consequently, if a single tree on a transect was occupied during all 3 surveys, or a different tree was occupied during each of 3 surveys, or 3 trees were occupied during a single survey only, each scenario would be considered a total of 3 colonies.

My motivation for analysis was to weigh evidence for competing hypotheses regarding the landscape-level ecological forces that affect colony abundance. Because the response variable, number of colonies, must be a positive integer, I followed the procedures in Atkins and Gallop (2007) to select from 4 of the most common regression models for count data: Poisson, negative binomial, zero-inflated Poisson (ZIP), and zero-inflated negative binomial (ZINB). The zero-inflated models are appropriate when the data includes many zeros. They are mixture models combining logistic regression to model excess zeros, also known as inflation, and negative binomial regression to model the count data (Lambert 1992). The biological interpretation is that logistic regression predicts areas of non-habitat (excess zeros) and negative binomial regression predicts the number of bat colonies in habitat identified by logistic regression.

I used likelihood ratio tests to compare nested models (i.e., Poisson to negative binomial and ZIP to ZINB). I used a qualitative test to compare non-nested models by comparing predicted counts from each model to the actual number of colonies. Comparing predicted counts from each model indicated that the data was highly zero inflated (Figure 5.2). The likelihood ratio test indicated the ZINB was superior to the ZIP ($\chi^2 = 6.64$, df = 1, $P = 0.010$).

Given that the number of colonies/transect varied between study sites, I considered a mixed effects ZINB model. Such a model can incorporate random effects variables, such as study sites, that have been drawn from a larger population of study sites (Min and Agresti 2005). I compared models with and without study site as a random effect using a likelihood ratio test and by qualitatively examining the residuals of each model. The model with random effects was superior to the model without random effects ($\chi^2 = 14.75$, df = 1, $P < 0.001$). Therefore, all models were developed as ZINB with random effects for study sites. All statistical analysis was performed in Program R 2.11.0 (R Core Development Team 2010) primarily using a function for mixed-effects ZINB models available from Atkins and Gallop (2007).

Because the ZINB model corresponds to two biological concepts, colony presence and colony abundance, I weighed evidence for two corresponding sets of hypotheses relating landscape-level forest characteristics to presence and abundance of Rafinesque's big-eared bat colonies. Specific hypotheses were that colonies would be present in areas of cypress-gum swamp (Clark 2003), or forested wetland (Chapter 1), or that colony presence would be random with respect to these habitats. Simultaneously, I compared hypotheses that, where present, colony abundance would be higher where foraging habitat is greater (Carter 2006), commuting costs are lower (Miles et al. 2006), water is available (Watrous et al. 2006), anthropogenic disturbance is lower (Sparks et al. 2005), alternate roosting habitat is greater (Brigham et al. 1997), wetlands retain water longer (Chapter 1), or that colony abundance would be random with respect to these factors. I also developed a global model of colony abundance, which included all uncorrelated (Pearson $R^2 < 0.25$) predictor variables. Forest characteristics associated with each hypothesis were determined by a literature review (Table 5.1). For analysis, I pooled data across years and excluded colonies found by radio tracking or *ad hoc* searches. I checked for adequate fit of the global model with a Pearson chi-square test and by comparing actual counts of colonies to the fitted values from the best model.

After creating the models, I used an information-theoretic approach (Burnham and Anderson 2002) to estimate relative strength of evidence for each model corresponding to a hypothesis. I used Akaike's Information Criteria (AIC; Akaike 1973) corrected for small sample bias (AIC_c; Hurvich and Tsai 1989) to assess evidence for models, with the lowest AICc indicating the best supported model. I evaluated the relative strength of evidence for each model by calculating AIC weights (w_i; Burnham and Anderson 2002), the probability that the i_{th} model is the best model of the candidate models. I used this approach to select the most parsimonious of the candidate models. I did not perform model averaging because it is not statistically appropriate for mixed models (Grueber et al. 2011). I calculated Nagelkerke's R^2 to quantify the variation explained by each model (Nagelkerke 1991).

I assessed model precision by calculating 90% confidence intervals for coefficients based on a *t*-statistic with *n*-1 degrees of freedom. For the zero-inflation portion of the results, I transformed the log-odds β coefficients to the probability of colony presence in each habitat type (Hosmer and Lemeshow 2000). For random effects, I exponentiated the log-odds β coefficients to obtain odds ratios that express how much more or less likely colony absence is at each site. For the count portion of the results, I exponentiated the β coefficients to obtain a factor expressing the effect of predictors as a percentage change in colony abundance, given that habitat is present. Confidence limits that encompass 0% indicate that estimates are not precise enough to conclusively determine the direction of the relationship between the predictor and colony abundance.

Roost-site Quantification and Spatial Modeling

I created a GIS database with 9 layers relevant to hypotheses generated during my literature review. I used 1:24,000 scale NWI wetland data (USFWS 2004) and 30 x 30 m resolution, 44-class landcover data (NARSAL 1998). The landcover type at the center of each transect was determined and a dummy variable coded the transect as cypress-gum swamp or other forest cover type. The NWI wetland category of each transect was coded with 2 dummy variables to encompass the 3 categories.

Bats may value roost sites that provide alternate roosts (Brigham et al. 1997), so I calculated percent of a 1000 m radius area around the transect center that was forested wetland because successive roosts are usually within that distance (Trousdale et al. 2008, Rice 2009). As an alternative measure or roosting habitat, I also calculated percent area that was cypress-gum landcover type. I approximated the amount of foraging habitat by calculating the percent of a 1000 m radius area around each transect that was pine (loblolly [*Pinus taeda*], slash [*P. elliottii*], shortleaf [*P. echinata*], or longleaf [*P. palustris*]) forest because most foraging bouts occur within 1000 m of the roost (Hurst and Lacki 1999, Menzel et al. 2001). To quantify the distance to travel corridors, water resources, and anthropogenic disturbance, I calculated the distance from the transect midpoint to the closest road open to vehicle passage, the closest permanent water source, and the closest urban area > 30 ha, according to the landcover data set. I also estimated the width of each NWI wetland by creating a 250 m radius buffer around transect midpoints. I then used the Spatial Analyst zonal geometry tool in ArcMap to approximate wetland width.

After characterizing habitat at the study sites, I exported the attributes for analysis in Program R. I applied the results of the best supported ZINB model to the attributes of each 30 m cell of spatial data to estimate colony abundance in each cell. Because the model predicts total colonies on a 1.5 ha transect after 3 surveys, and spatially explicit abundance was estimated as total colonies on 0.09 ha after 1 survey, I multiplied the results by 0.09/1.5/3 to obtain the proper units. I summed abundance in all cells to obtain total abundance estimates. I used bootstrapping with 10,000 replicates to estimate 90% confidence intervals for the number of colonies. I also mapped the best supported ZINB model by applying the model to each 30 m raster cell, using the Spatial Analyst raster calculator in ArcMap.

Estimated colony numbers based on surveys of trees with basal hollows are biased low for two reasons. First, observers may fail to detect bats that are present (MacKenzie et al. 2002). Second, some bats roost in trees without basal hollows (Trousdale and Beckett 2005). To account for imperfect detection, I divided estimates of the number of colonies by 0.955, an estimate of the detection probability (Chapter 1). To account for bats roosting in trees without basal hollows, I divided by 0.667, an estimate of the days that radio tagged bats spent in trees with basal hollows in a concurrent study (M. Clement, unpublished data). Correcting for these two factors yielded a corrected estimate of colonies on the 8 sites.

I estimated the number of bats in these colonies by multiplying colonies in each wetland category by average colony size in that wetland category. I did not directly model the number of bats with the ZIP model because the distribution was bimodal (one peak for small male colonies and one peak for large female colonies) and therefore not conducive to modeling. I calculated density by dividing number of colonies or bats by ha of forested wetland.

RESULTS

I searched 123 transects during 2007 and 2008. Forty-one transects were occupied by 179 bat colonies containing 512 bats. Transects with bats were characterized by narrow, semi-permanently flooded wetlands, and cypress-gum swamps (Table 5.2). I found colonies at all study sites, although the number of colonies/transect varied among sites by a factor of 25. I excluded swamp landcover from the global model because it was correlated with wetland category ($R^2 = 0.36$). The Pearson chi-square goodness-of-fit test for the global model was not significant, indicating a good fit between the model and the data ($\chi^2 = 7.72$, df = 8, $P = 0.461$).

The best supported model predicted the presence of bat habitat from wetland categories and the number of colonies from wetland width (Table 5.3). This top model received 95.5% percent of the AIC weight and therefore was the only model in the confidence set. The results indicated that semi-permanently flooded wetland was twice as likely as seasonally flooded wetland and 20 times as likely as saturated wetland to be appropriate roosting habitat (Table 5.4).

Study sites differed substantially in the probability of forested wetlands being suitable habitat for bats, with wetlands at the best site being 12.1 times as likely to be suitable, and wetlands at the worst site being 3.1 times less likely to be suitable, relative to an average site. Furthermore, within appropriate habitat, wetland width had the greatest effect on colony abundance, reducing colony abundance by 6.0% for every 10 m increase in width (Figure 5.3).

Extrapolated to the full area of the 8 study sites, the best supported model estimates that the sites held 2,190 colonies (bootstrap 90% confidence interval of 1,619 to 2,969), or 0.14 colonies/ha for the 3 wetland categories combined (Table 5.5). Using the average number of bats per colony found in each wetland category, I estimate there were 6,032 bats (4,572 to 8,059) on the study sites or 0.38 bats/ha. Based on my estimate that I detected only 95.5% of colonies, the corrected estimate would be 2,293 colonies. Further correcting for the number of colonies not detected because they were in trees without basal hollows (33.3%), the final estimate was 3,438 colonies.

Average predicted density in semi-permanently flooded wetlands was 0.27 colonies/ha and 1.15 bats/ha, while the density in saturated wetlands was 0.04 colonies/ha and 0.04 bats/ha (Table 5.5). Density varied among study sites, ranging from 0.08 colonies/ha of wetland and 0.16 bats/ha of wetland at Little Satilla WMA to 0.21 colonies/ha of wetland and 0.66 bats/ha of wetland at Moody Forest. Density patterns varied as well (Figure 5.4). Clayhole Swamp WMA, Chickasawhatchee WMA, and River Bend WMA all have substantial amounts of wide, semi-permanently flooded wetlands predicted to support medium colony density (0.10-0.50 colonies/ha). Beaverdam WMA, Moody Forest, Ocmulgee WMA, and Tuckahoe WMA all have large areas of saturated wetlands predicted to support low colony density (0.01-0.10 colonies/ha) and small areas of narrow, semi-permanently flooded wetlands predicted to support high colony density (0.51-1.60 colonies/ha). Few colonies were found at Little Satilla WMA and predicted densities are generally low (Figure 5.4).

DISCUSSION

Few abundance or density estimates have been published for bats that do not roost in caves, partly because such roosts are typically located by radio-telemetry (Barclay and Kurta 2007). The primary exceptions are studies of foliage roosting tropical megachiroptera and bats roosting in tents or furled leaves (Hayes et al. 2009). Megachiroptera can be relatively large and noisy and often defoliate roost trees, making them relatively conspicuous (Wiles et al. 1991). Surveys of megachiroptera are typically conducted from vantage points, rather than along transects, and sometimes use *ad hoc* corrections for imperfect detection (Utzurrum et al. 2003). A review of surveys of megachiroptera in U.S. Pacific territories found densities up to 1 bat/ha (Utzurrum et al. 2003). Surveys for tent roosting bats involve searching all appropriate leaf structures in a small area with an assumed detection rate of 1 (Findlay and Wilson 1974, Foster 1992). These surveys covered ≤8 ha and yielded 1 to 22 bats/ha, with no attempt to extrapolate beyond survey plots (Findlay and Wilson 1974, Foster 1992). Others have systematically surveyed potential roosts for bats without reporting abundance estimates (Storz et al. 2000, Chaverri and Kunz 2006). Additionally, a few studies have estimated abundance using mark-recapture techniques on bats captured in mist nets (Morrison 1978, Heideman and Heaney 1989) or during roost searches (Vonhof and Fenton 2004). Given bat populations' vulnerability to decline, more measurement of bat abundance is essential to science-based management (O'Shea et al. 2003).

Although Rafinesque's big-eared bat often roosts in cypress-gum swamps (Clark 2003), models predicting roosting habitat from forested wetland categories received more support from my data. Wetland category is likely a more powerful predictor because Rafinesque's big-eared bat commonly roosts in water tupelo (Carver and Ashley 2008), which are found in flooded areas within forested wetland habitats (Hook 1984). I found water tupelo prevalence was closely related to wetland categories, with water tupelo composing 4% of hollow trees in saturated wetlands, 50% in seasonally flooded wetlands, and 75% in semi-permanently flooded wetlands. Additionally, silvicultural best management practice guidelines in Georgia proscribe harvesting within sloughs (Georgia Forestry Commission 2009). As a result, sloughs often contained large trees, which are used by Rafinesque's big-eared bats (Ashley and Carver 2008), while surrounding areas contained few large trees (Figure 5.5).

Although colony abundance was higher in narrower wetlands, it seems unlikely that bats are attracted to wetlands based on their width, *per se*. Rather, wetland width likely was a surrogate for water persistence as narrow wetlands tended to be deeper sloughs that held water longer during summer, even if they were categorized as seasonally flooded in the NWI. Wider wetlands tended to be floodplains that held water for shorter periods of time, even if classified as semi-permanently flooded. Effectively, the width variable served as a supplement to the wetland category variable, with narrow wetlands more likely to be flooded. The narrow, flooded wetlands provide the conditions for an abundant supply of hydrophilic tree species, such as water tupelo (Hook 1984), resulting in higher colony abundance.

Wetland category and width have not been used in predictive geographic models of bat presence. The most common significant predictors have been forest area (Jaberg and Guisan 2001, Greaves et al. 2006, Watrous et al. 2006, Rebelo and Jones 2010) and elevation (Jaberg and Guisan 2001, Duff and Morrell 2007, Rebelo and Jones 2010) followed by temperature (Greaves et al. 2006, Rebelo and Jones 2010), water (Jaberg and Guisan 2001, Duff and Morrell

2007), and development (Jaberg and Guisan 2001, Rebelo and Jones 2010). Forest area and distance to water were not valuable as predictors in my study, perhaps because both were abundant and also because forested wetland categories provided more precise habitat descriptions. Although Rafinesque's big-eared bat has been reported to avoid developed areas (Jones 1977), there was little development on the study sites, making it a poor predictor. I did not explore elevation or temperature because I expected little variation across the study sites, while studies in mountainous regions encompassed areas of high variability (e.g., Jaberg and Guisan 2001).

Rafinesque's big-eared bat is generally considered uncommon throughout its range (Barbour and Davis 1969, Harvey et al. 1999), although in certain areas it may be captured in greater numbers than other bat species (Medlin and Risch 2008, Clement and Castleberry, in press) suggesting that it may be locally common. Published articles have reported locating 4 to 44 tree roosts at study sites (Lance et al. 2001, Gooding and Langford 2004, Mirowsky et al. 2004, Carver and Ashley 2008). A summary of unpublished surveys reported numerous sites with 5 to 45 tree roosts each (Clark 2003), while more recent surveys have identified 35 to 49 tree roosts per site (Stevenson 2008, Lucas 2009, Rice 2009). Tallying records such as these, as well as bats in caves and anthropogenic roosts, the total population has been estimated as <10,000 adults (Arroyo-Cabrales and Ticul Alvarez Castaneda 2008). I located between 2 and 44 tree roosts on each study site by sampling a small portion of forested wetlands, but extrapolating to the entire area indicated 6,032 bats were present on 16,016 ha. This estimate suggests that more than 10,000 bats exist range-wide.

My results indicated there was a strong site-specific effect, with some sites more likely to have bats present on a transect. The difference in colony density across sites was likely due to differences in the prevalence of large, hollow water tupelo among sites. However, tree size and decay were not reflected in the spatial data used for analysis, and therefore the unmeasured variation resulted in a site-specific effect. Some studies have found that radio-tagged bats were more likely to roost in forests with a greater number of available preferred roost structures (Crampton and Barclay 1998, Russo et al. 2004). Similarly, Rafinesque's big-eared bats probably select individual trees that meet their roosting needs and therefore achieve greater density where more roosts are available. Variation in the number of large, hollow water tupelo between sites was likely due to differences in historical land use and the natural range of water tupelo. Tree harvesting typically results in low densities of large, hollow trees (Graves et al. 2000, Wilhere 2003) and harvests likely varied across study sites given their wide dispersion and different owners. I did not document the history of the sites, but they had different owners, who presumably managed the properties for different purposes. Additionally, Little Satilla WMA lies outside the core range of water tupelo (Johnson and Beaufait 1965). As a result, only 16.5% of surveyed hollow trees at that site were water tupelo, compared to 60.4% at the other sites combined. Other bats, such as the New Zealand long-tailed bat (*Chalinolobus tuberculatus*) are also less likely to be present outside the range of preferred roost tree species (Greaves et al. 2006). Overall, the substantial differences between sites caution that extrapolations beyond the 8 study sites might be imprecise. However, for a site inside the range of water tupelo and with a homogenous land use history, the model should identify areas of greatest suitability for Rafinesque's big-eared bat.

MANAGEMENT IMPLICATIONS

My modeling results can be used to identify potential habitat for Rafinesque's big-eared bat from GIS data. Although I found considerable variability within and among sites surveyed, predictions generated from the model provide information about priority areas for future surveys and a framework for designing efficient surveys. To increase efficiency by focusing efforts on the areas of greatest colony density, surveys should target the narrowest seasonally flooded and semi-permanently flooded wetlands present. However, I caution that past land-use history has influenced current site conditions and should be considered when evaluating sites and designing surveys. Additionally, my survey methods could be used to estimate bat abundance on additional sites and for additional species. If repeated, these abundance estimates could reveal changes in abundance, which could be used by wildlife managers to assess species status and evaluate management activities.

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Table 5.1: Hypothesized factors affecting roost presence and abundance, model variables, and references for summer roosts of Rafinesque’s big-eared bat (*Corynorhinus rafinesquii*) in the Coastal Plain of Georgia, 2007-2008.

Hypothesis	**Model Variables (predicted effect)**	**Example Reference**
Roost Presence Factor		
Roosts available	Land cover type (+)	Greaves et al. 2006
Roosts available	Wetland type (+)	Watrous et al. 2006
Random	none	none
Roost Abundance Factor		
Foraging habitat	Area of pine forest (+)	Menzel et al. 2001
Commuting cost	Distance to roads (-)	Miles et al. 2006
Water available	Distance to water (-)	Watrous et al. 2006
Anthropogenic disturbance	Distance to urban (+)	Sparks et al. 2006
Wetland persistence	Wetland type (+)	proposed
Wetland persistence	Wetland width (-)	proposed
Alternate roosts	Area of cypress-gum swamp (+)	Brigham et al. 1997
Alternate roosts	Area of flooded wetland (+)	Brigham et al. 1997
Random	none	none
Global model	all of the above, excluding area of cypress-gum swamp	All of the above

Table 5.2: Mean and standard deviations (SD) of variables measured on transects with and without Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) roost trees in the Coastal Plain of Georgia, 2007-2008.

	Unoccupied (n=82)		Occupied (n=41)	
Variable	$\overline{X}$	SD	$\overline{X}$	SD
Cypress-gum (Y/N)	0.59	0.50	0.80	0.40
Semi-permanently flooded (Y/N)	0.40	0.49	0.68	0.47
Seasonally flooded (Y/N)	0.29	0.46	0.29	0.46
Saturated (Y/N)	0.30	0.46	0.02	0.16
Distance to roads (m)	453	440	494	415
Distance to water (m)	628	467	509	338
Distance to urban (m)	8,865	3,833	9,778	4,763
Wetland width (m)	212	125	131	97
Area pine (%)	18.7	13.8	14.5	9.7
Area swamp (%)	43.0	22.1	41.1	21.2
Area wetland (%)	41.0	24.4	33.9	22.1

Table 5.3: Zero-inflated negative binomial (ZINB) models used to predict Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) colony abundance-habitat relationships in the Coastal Plain of Georgia, 2007-2008. Variables, number of parameters in the model (K), Akaike's Information Criterion adjusted for small sample size (AICc), difference in AICc between a model and the model with the lowest AICc (ΔAICc), model weights (wi), and Nagelkerke's R2 values. Colony presence refers to the logistic portion of the ZINB model and colony abundance refers to the Poisson portion of the ZINB model. Study site was included as a random effect in the colony presence portion of all models.

Colony Presence Variables	**Colony Abundance Variables**	**K**	**AICc**	**ΔAICc**	w_i	R^2
Wetland forest type	Wetland width	7	313.52	0.00	0.955	0.357
Wetland forest type	Pine forest area	7	321.47	7.95	0.018	0.310
Wetland forest type	Wetland forest area	7	322.60	9.08	0.010	0.303
Wetland forest type	Global	14	322.92	9.40	0.008	0.399
Wetland forest type	None	6	325.48	11.96	0.002	0.271
Wetland forest type	Cypress-gum swamp area	7	325.80	12.28	0.002	0.283
Wetland forest type	Distance to roads	7	326.32	12.80	0.002	0.280
Wetland forest type	Distance to water	7	327.48	13.96	0.001	0.273
Wetland forest type	Distance to urban	7	327.56	14.03	0.001	0.272
Wetland forest type	Wetland forest type	8	329.25	15.73	0.000	0.276
Land cover type	Global	13	329.91	16.39	0.000	0.346
None	Global	12	338.67	25.14	0.000	0.277
None	None	4	357.33	43.81	0.000	0.000

Table 5.4: Coefficient estimates, standard errors, percent probability, percent change, and 90% upper and lower confidence intervals (CI) for the top model predicting roost abundance of Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) in the Coastal Plain of Georgia, 2007-2008.

Model Portion/Variable	**Coefficient**	**Standard Error**	**Probability Appropriate Habitat**	**Change in Colony Abundance, Given Presence**	**Lower CI**	**Upper CI**
Logistic						
Semi-permanently flooded	-0.314	0.477	57.8%		38.4%	75.0%
Seasonally flooded	1.178	0.572	29.7%		7.0%	70.3%
Saturated	3.800	1.169	3.0%		0.0%	31.5%
Negative binomial						
Intercept	2.069	0.205				
Wetland width (10 m units)	-0.062	0.015		-6.0%	-8.3%	-3.7%

Table 5.5: Wetland area, number of colonies, colony density, number of bats, and bat density by study site and by wetland category for Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) in the Coastal Plain of Georgia, 2007-2008.

Location	**Area (ha)**	**No. of Colonies**	**Colony Density**	**No. of Bats**	**Bat Density**
Site					
Beaverdam	1,259	106	0.084	340	0.270
Chickasawhatchee	4,117	667	0.162	2,280	0.578
Clayhole Swamp	1,558	171	0.110	600	0.385
Little Satilla	2,111	176	0.084	330	0.156
Moody Forest	588	125	0.212	388	0.660
Ocmulgee	1,358	220	0.162	632	0.465
River Bend	1,043	97	0.093	291	0.279
Tuckahoe	3,983	627	0.158	1,070	0.290
Total	16,016	2,190	0.137	6,032	0.377
Wetland Type					
1A	6,309	269	0.043	269	0.043
1C	5,763	839	0.146	1,235	0.215
1F	3,944	1,082	0.274	4,528	1.148
Total	16,016	2,190	0.137	6,032	0.377

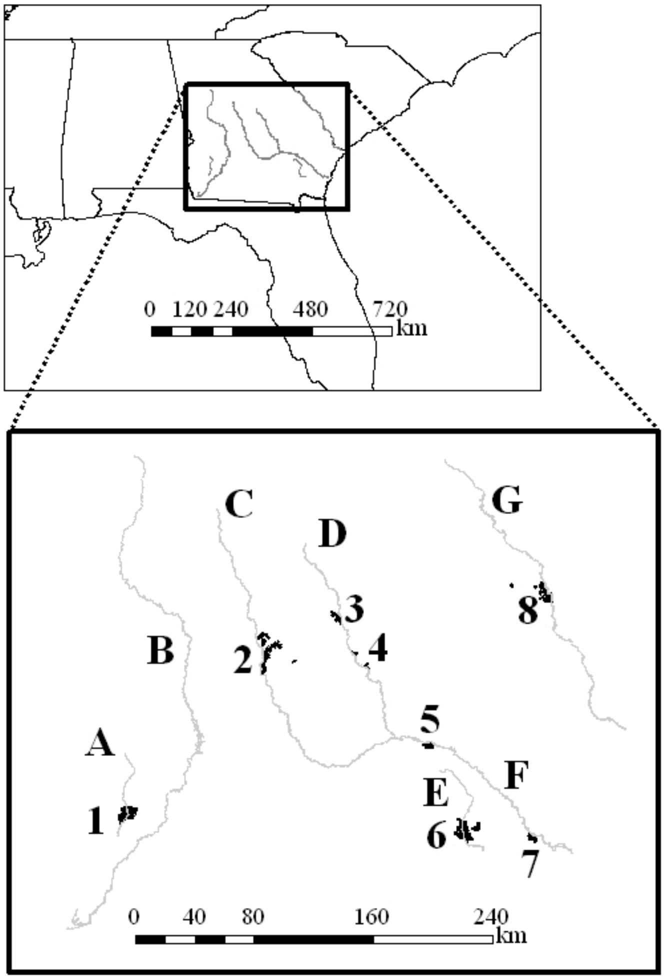

Figure 5.1: Map showing study sites and associated river systems in the Coastal Plain of Georgia, USA used to examine summer colony density by Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) in 2007-2008. River systems are denoted by letters (A=Chickasawhatchee Creek, B=Flint River, C=Ocmulgee River, D=Oconee River, E=Little Satilla River, F=Altamaha River, G=Savannah River) and study sites are denoted by numbers (1=Chickasawhatchee Wildlife Management Area [WMA], 2=Ocmulgee WMA, 3=Beaverdam WMA, 4=River Bend WMA, 5=Moody Forest Natural Area, 6=Little Satilla WMA, 7=Clayhole Swamp WMA, 8=Tuckahoe WMA).

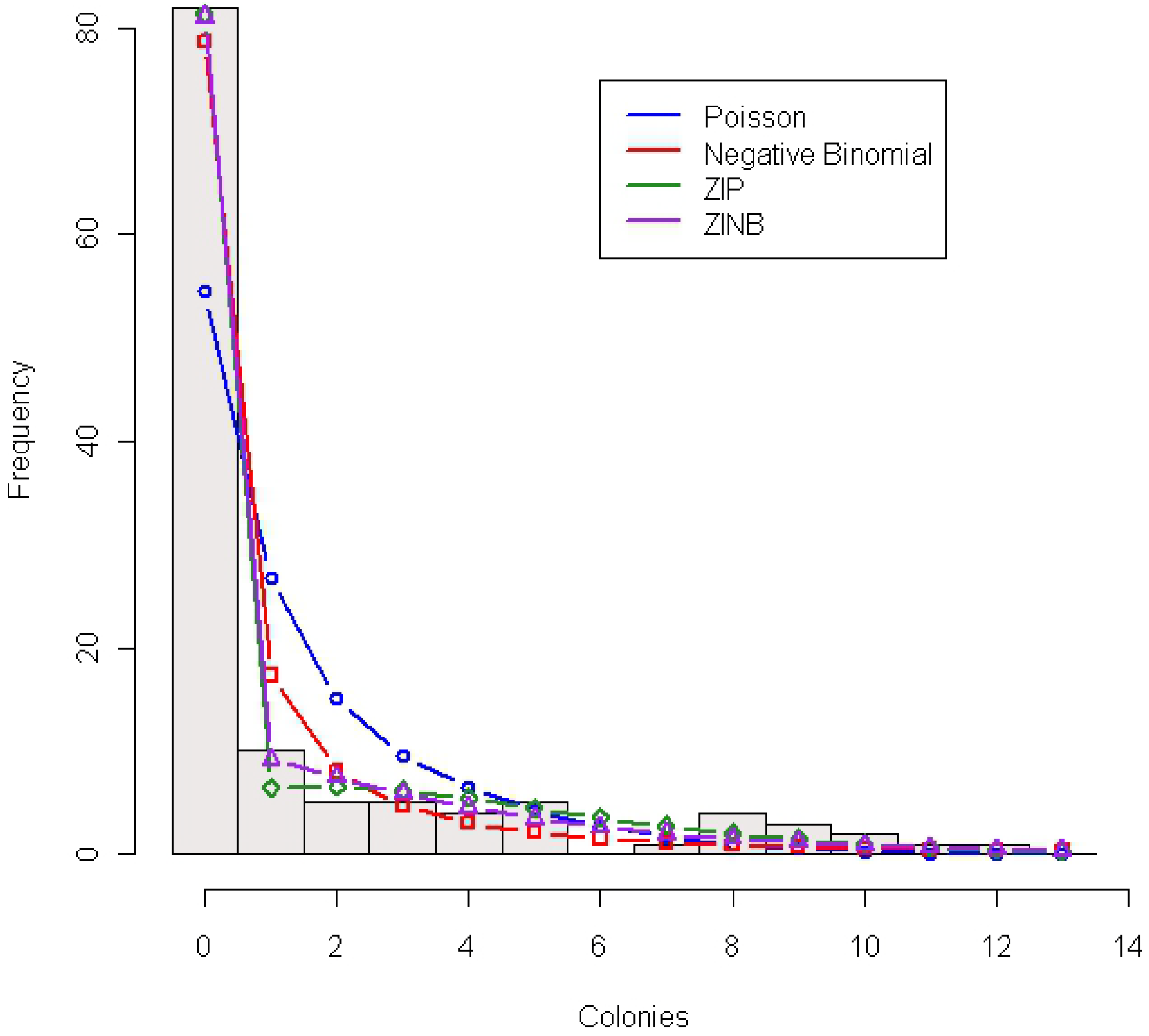

Figure 5.2: Actual (bars) and predicted (lines) number of colonies of Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) using Poisson, negative binomial, zero-inflated Poisson (ZIP), and zero-inflated negative binomial (ZINB) regression models. Data were collected in the Coastal Plain of Georgia, 2007-2008.

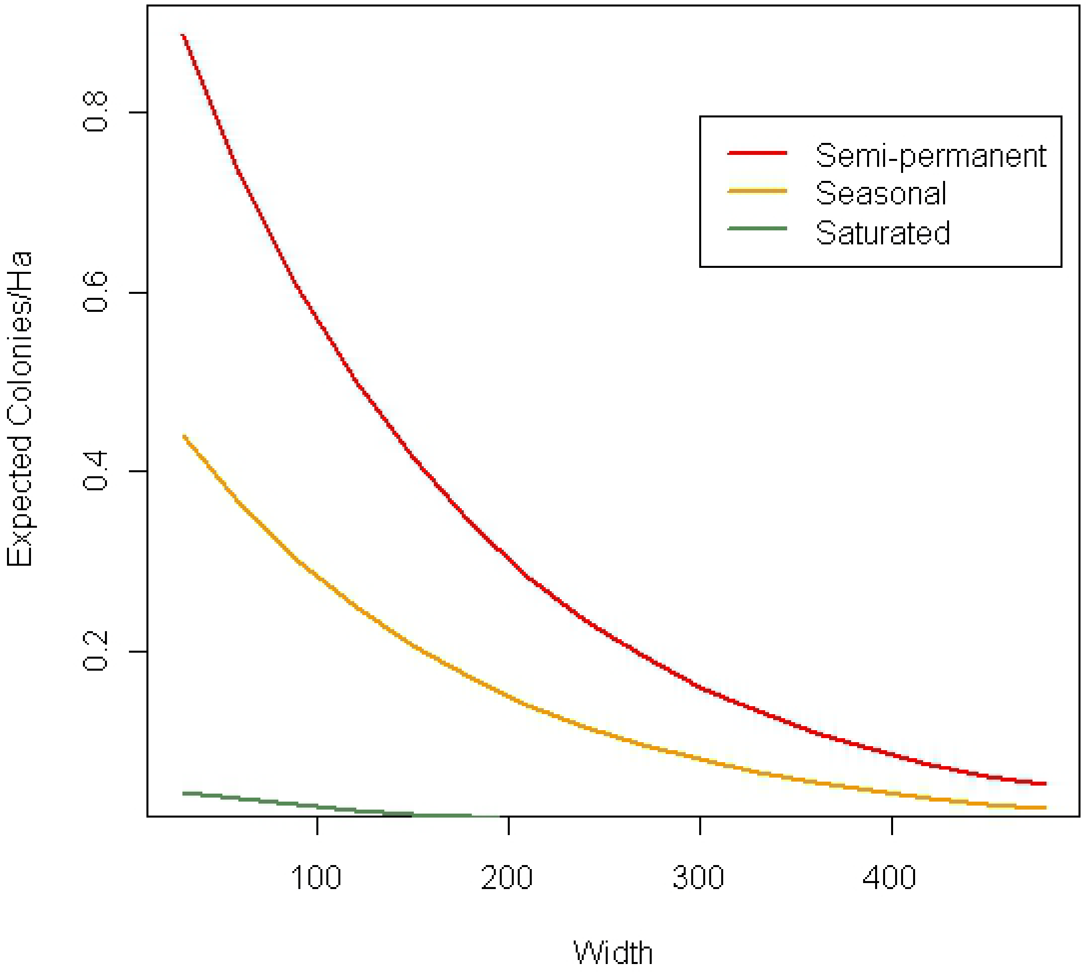

Figure 5.3: Predicted density (colonies/ha) for Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) in wetlands of different hydroperiod and width. Predictions are based on best supported zero-inflated negative binomial regression model of data collected in the Coastal Plain of Georgia, 2007-2008.

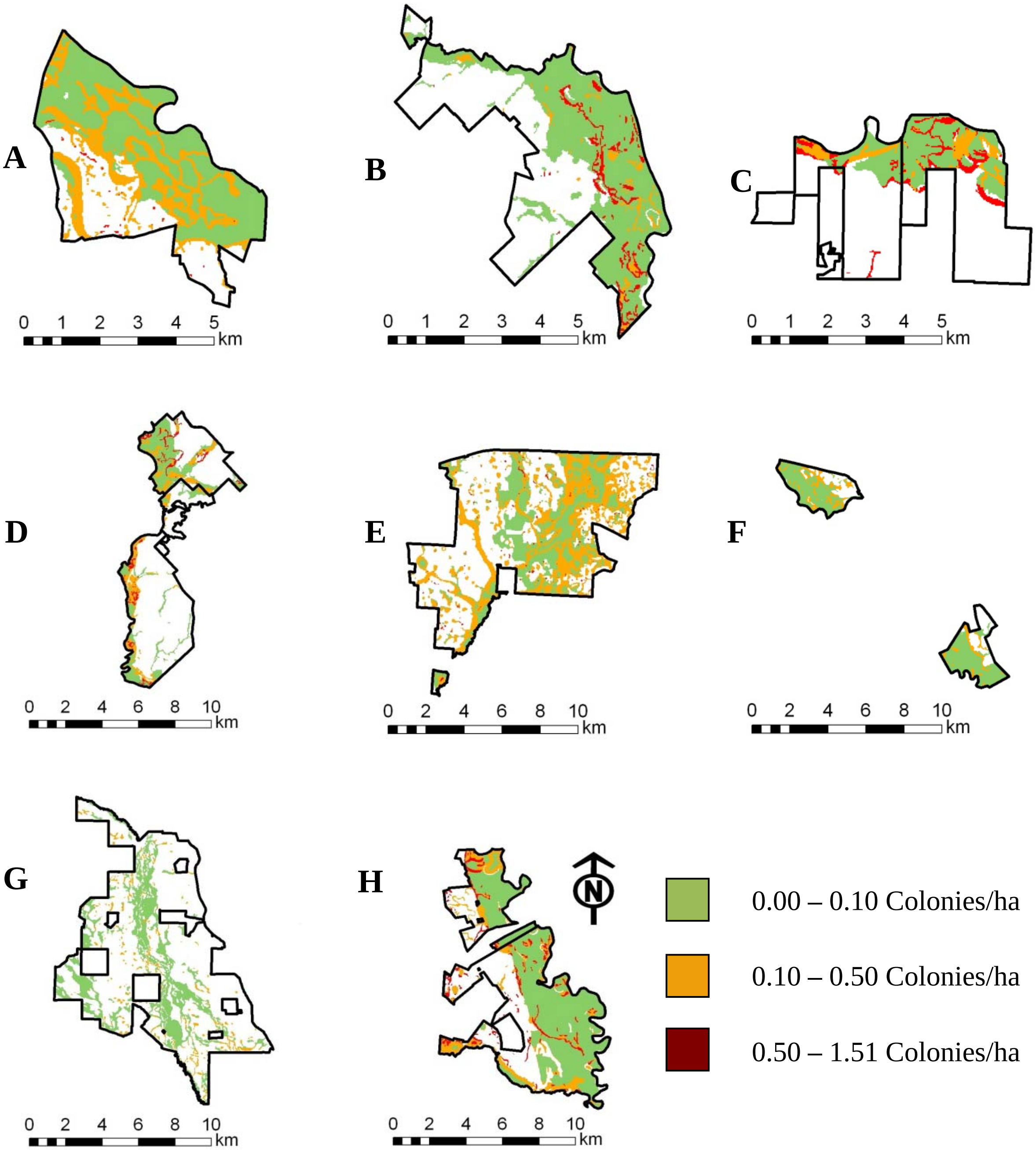

Figure 5.4: Colony density maps produced from landscape level zero-inflated negative binomial modeling for Rafinesque’s big-eared bats (*Corynorhinus rafinesquii*) in the Coastal Plain of Georgia, 2007-2008. A) Clayhole Swamp Wildlife Management Area (WMA), B) Beaverdam

WMA, C) Moody Forest Natural Area, D) Ocmulgee WMA, E) Chickasawhatchee WMA, F) River Bend WMA, G) Little Satilla WMA, H) Tuckahoe WMA.

Figure 5.5: Tree within sloughs on publically managed land in the Coastal Plain of Georgia frequently have large diameters and well developed hollows (foreground), while trees outside of sloughs are usually much smaller (background).

CHAPTER 6

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

In recent decades, studies of bat summer tree roosts have advanced from anecdotal observations to systematic studies focused on tree roost selection (Barclay and Kurta 2007). Many studies have followed the protocol of locating roosts by radio-telemetry and then comparing the external characters of occupied and available trees (Willis and Brigham 2007, Barclay and Kurta 2007). These studies indicate that tree-roosting bats typically select large diameter trees with low canopy cover during summer (Kalcounis-Ruppel et al. 2005). However, a few studies have suggested that internal cavity characteristics may play a larger role in roost selection than external characters (Sedgeley and O'Donnell 1999, Parsons et al. 2003). The trend towards large roost trees with low canopy cover is often interpreted as an indication that the need for a favorable microclimate is the ultimate force in roost selection (Brigham 2007). While there is indirect evidence that microclimate affects summer tree roost selection, few studies have provided direct evidence for the hypothesis (Boyles 2007). While roost selection has been the focus of many recent studies, the most common radio telemetry protocol is insufficient for estimating abundance of bats (Weller 2007). Therefore, my aim was to use an alternate protocol to search transects for conspicuous roosts of Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) and southeastern myotis (*Myotis austroriparius*) and estimate the importance of internal cavity characters to roost selection, the importance of cavity microclimate to roost selection, and abundance of bats across study areas.

TREE ROOST STRUCTURE

Tree cavity roosting bats are commonly hypothesized to select roosts that provide a favorable microclimate (Barclay and Kurta 2007). If this were the case, bats could be expected to select roosts with large solid wood volume (Sedgeley 2001), low canopy cover (Brigham et al. 1997), and certain tree species (Boyles 2007) based on the presumed effect on cavity microclimate. In contrast, I found that Rafinesque's big-eared bats were most likely to roost in trees with large cavity volumes and smooth interior walls during the summer, with maternity colonies found in even larger roosts than bachelor colonies. My results were most consistent with the hypothesis that bats select roosts that allow them to avoid predators. Large cavities allow bats to attain evasive flight without leaving the roost (Gellman and Zielinski 1996) if terrestrial predators enter the roost, while smooth surfaces are difficult for predators to climb (Mullin and Cooper 2002). In contrast with Rafinesque's big-eared bats, the best supported hypothesis for southeastern myotis roost selection was the microclimate hypothesis. However, none of the tree structure variables were significant predictors of bat presence. The single best predictor was study site, with bats far more common in Chickasawhatchee WMA. Therefore, my result provided only weak evidence that southeastern myotis select summer roost trees based on microclimate.

In other studies, bat roosts are more commonly described by diameter at breast height (dbh) than cavity volume or solid tree volume. Because all 3 variables are correlated, my results are consistent with studies reporting southeastern myotis and Rafinesque's big-eared bat in large and very large dbh roosts, respectively (Carver and Ashley 2008). However, cavity volume and solid tree volume were better at distinguishing roost trees, which is consistent with the few studies that measured cavity volume found it a better predictor of use than dbh (Gellman and Zielinksi 1996, Parsons et al. 2003, Willis et al. 2006). Therefore, cavity characteristics may be important to roost selection across a wide variety of species and should be measured, if feasible.

The fact that these bat species provided weak or no support for the microclimate hypothesis could be because southern Georgia is warmer during the summer than higher latitude areas where roost selection and microclimate have been studied (Sedgeley 2001, Willis and Brigham 2007). Furthermore, roost openings were unusually close to the ground (Kalcounis-Ruppell et al. 2005), which may mean these species face greater selective pressure from predators, relative to other bat species (Arendt 1986). The fact that these species selected different roosts could be due to competition between the species, differences in roosting behavior (Stevenson 2008), or the greater flight agility of Rafinesque's big-eared bat in small spaces (Jones and Suttkus 1971). One implication of the inability of tree structure to predict presence of southeastern myotis is that an unidentified factor affected bat presence.

Although individual trees with large cavity volumes and large solid wood volumes were most commonly used, any cypress-gum swamp stand with many large dbh trees should include a number of suitable roost trees. Therefore, wildlife managers seeking to promote Rafinesque's big-eared bat and southeastern myotis should value trees with large cavities and wood volumes, but may find it more practical to identify trees with large dbh's. Given that it could take >100 years for trees to reach adequate sizes (Johnson and Beaufait 1965), it is essential to protect suitable wetland habitat within these species' ranges containing both large trees and smaller trees that will become suitable in coming decades. Given that most roosts were in water tupelo, it is also important for land managers to maintain the natural flooding regime essential to maintaining populations of these trees (Hook 1984). It has been reported that thinning does (Goelz et al. 2001) and does not (Kennedy 1983) increase growth rates of water tupelo. Removing competing tree species also may not increase growth rates (Goelz et al. 2001). Data on coppice regeneration is also conflicting, with both high (Aust et al. 2006) and low (Keim et al. 2006) survival of sprouts being reported. The success of sprouts may depend on stump characteristics (Gardiner et al. 2000). In areas affected by land subsidence and construction of canals and levees, increased flood duration may severely impact forest regeneration (Conner and Day 1988). Therefore, maintaining wetland hydroperiod may contribute more to the promotion of roosting habitat than common silivicultural methods.

TREE ROOST MICROCLIMATE

I found that tree structure affects tree cavity microclimate in large, hollow trees in swamps, but that cavity microclimate has little effect on presence of Rafinesque's big-eared bat during the summer. While dbh and canopy cover are often expected to be important predictors of cavity microclimate (Kalcounis-Ruppell et al. 2005), I found that temperature was most affected by the number and type of entrance holes, while humidity was most affected by canopy cover. However, even these structures explained <25% of microclimate variation. Similarly, position within the cavity explained little of microclimate variation within a cavity. Studies which found more impact on microclimate from dbh and canopy have occurred at higher latitudes (Wiebe 2001), with lower canopy cover (Vonhof and Barclay 1997), thicker cavity walls (Sedgeley and O'Donnell 1999), and less water, which may enhance the effect of dbh and canopy on cavity microclimate.

Despite microclimate varying among available trees, I found no evidence that Rafinesque's big-eared bats selected roosts on the basis of microclimate. While several studies have concluded that microclimate is important to bat tree roost selection (Vonhof and Barclay 1997, Kalcounis and Brigham 1998, Sedgeley 2001, Ruczynksi 2006), big brown bats in Saskatchewan were indifferent to roost microclimate because social thermoregulation was more important (Willis and Brigham 2007). The discrepancy between my result and the general expectation that microclimate is important may be due to study site latitude, insect availability, alternate selective pressures, or the particular bat studied. Many of the studies proposing microclimate as an important roost selection factor have occurred in Canadian forests (e.g., Vonhof and Barclay 1997, Kalcounis and Brigham 1998), where temperatures are lower and summer days are longer. Under those conditions, bats may well select roosts based on microclimate. However, the subtropical climate in Georgia may reduce thermoregulatory stress and make microclimate inconsequential in the Coastal Plain (Kunz and Lumsden 2003). Georgia also has longer and warmer nights than high latitude areas, which may support more insect abundance and reduce thermoregulatory constraints. Furthermore, the conspicuous and accessible roosts used by Rafinesque's big-eared bats may increase the threat from predators and force bats to select roosts that provide room to evade predators (Lewis 1995). Finally, physiology varies between bat species and therefore different species may have different roost selection criteria (Webb et al. 1995).

Efforts to provide habitat for Rafinesque's big-eared bat should focus on tree cavity size and not cavity microclimate. In designing artificial roosts for this species, cavity size is likely to be most important, as long as microclimate is within the broad range observed in natural roosts. Furthermore, investigations of bat tree roost selection should consider multiple competing hypotheses, including, but not limited to roost microclimate.

ABUNDANCE AND DISTRIBUTION

Forest that was flooded for the greatest duration was most likely to be occupied by Rafinesque's big-eared bat during the summer. Within areas occupied by bats, the narrowest wetlands held the most bats, possibly because wide floodplains generally held water for shorter durations than narrow sloughs. Using the best supported model, I estimate that my study sites held 2,190 colonies, or 0.14 colonies/ha of wetland and 6,032 bats, or 0.38 bats/ha of wetland.

Abundance estimates are rare for tree roosting bats. For Rafinesque's big-eared bat, published articles have reported minimum population sizes of 4 to 44 colonies (Lance et al. 2001, Gooding and Langford 2004, Mirowsky et al. 2004, Carver and Ashley 2008). A summary of unpublished surveys reported numerous sites with 5 to 45 colonies (Clark 2003), while more recent surveys have identified 35 to 49 colonies per site (Stevenson 2008, Lucas 2009, Rice 2009). Considering these records, as well as bats in caves and anthropogenic roosts, the total population had previously been estimated as <10,000 adults (Arroyo-Cabrales and Ticul Alvarez Castaneda 2008). Given my estimate of 6,032 bats on my study sites, this number is likely too low.

My modeling results could be used to identify potential habitat for Rafinesque's big-eared bat from GIS data. To increase efficiency by focusing efforts on the areas of greatest colony density, surveys should target the narrowest seasonally flooded and semi-permanently flooded wetlands present. However, land-use history influences current site conditions and should be considered when designing surveys.

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