Chapter 2: Natural History and Habitat Requirements

Natural History

Reproduction and Longevity

Though there is often very little courtship behavior involved in the mating of bats, male and females in North America often gather in swarms at the entrance of hibernacula or autumn roosts to mate between late summer and early winter (Barbour and Davis 1969, Thomas et al. 1979). However, mating may also occur within hibernacula during periods of arousal from hibernation in some species. Delayed ovulation and fertilization are common reproductive methods used by bats, and occur when sperm is stored in the oviduct over winter and the egg is fertilized in late winter or early spring. One of the exceptions to this is the Brazilian free-tailed bat, which does not store sperm over winter but mates in mid-Feb to late March. Gestation for about half the bats in South Carolina lasts between 40 and 60 days and 20 to 30 days longer for the Brazilian free-tailed bat, Rafinesque's big-eared bat, eastern red bat, hoary bat, and Seminole bat.

The number of young produced by bat species of South Carolina varies from one to five, though most species have an average of two per year. However, all *Myotis* species in the state except for the southeastern bat give birth to one young per year. Most bats in South Carolina are born between May and June. Even though silver-haired bats are a migrant and may give birth in more northern portions of their range, there are records of silver-haired bats in the northwest corner of South Carolina in April and July (Webster 2013). Any parturition in those areas would be expected in June and July.

Newborn bats are completely dependent on their mother for care, and are naked and pink-skinned (Kunz and Kunz 1987). Young are generally left in a nursery roost, often in a crèche with other young, while the mother forages. For five bat species of South Carolina where the duration is known, lactation generally lasts between four to six weeks. Most young usually become volant (able to fly on their own) between three to five weeks, and in six species are weaned between three to nine weeks. For most species in South Carolina, males and females usually become sexually mature within their first year of life.

The bats found in South Carolina have a life span that varies by species from an average of two years in the evening bat to a maximum of 30 years in the little brown bat. This is particularly amazing because, for example, most small rodents the size of the eastern small-footed bat only live around 1.5 years while the eastern small-footed bat may live up to eight times longer. Accurate survival rates on most species of bats in the state are unknown. As is true for many animals, the survival rates in North American bats have been shown to be higher in adults at 63-90% than in juveniles at 23-80% (Tuttle and Stevenson 1982, Frick et al. 2007, 2010*b*, O'Shea et al. 2010, 2011).

Echolocation

Echolocation is a highly evolved process whereby a bat emits an ultrasonic sound and processes the echo from that sound in order to identify objects in its immediate environment. This ability is what allows bats "see" in total darkness, though bats are not blind and many have excellent vision. The ultrasonic sounds used are created as air passes over the vocal cords in the larynx, and then emitted through the mouth or nostrils at frequencies between 20 kHz and 120kHz. These high frequency sounds are above the range of human hearing, and have relatively short wavelengths that serve to best detect small prey items. Additionally, because short wavelengths don't travel far, it may help bats avoid interference from the echolocation of other bats. Bats have large, highly adapted ears that allow them to hear returning echoes from high frequency sounds bouncing off objects such as insects in their environment. Just inside and at the base of their ear is a cartilaginous projection known as the tragus that may help to improve the directionality or sensitivity to incoming echoes (Altringham 2011). In general, bats use echolocation to track the movements of prey by emitting short pulses of sound separated by longer periods of silence, processing the echoes returned to them, determining the distance to their prey, and emitting more pulses of sound to track and eventually capture their prey (Arita and Fenton 1997). More specifically, there are different phases associated with prey capture whereby bats change the length, absolute frequency and bandwidth (range of frequencies) of their pulses. When a bat is looking for prey during the search phase, their sound pulses are longer, have more time in between each pulse, and may be emitted at lower frequencies in order to travel further and cover a larger search area. When prey is detected, the approach phase occurs, whereby the bandwidth of the pulses increases and become faster and shorter together to avoid overlap as the bat approaches its target. During the last or terminal phase, the pulses become even faster, shorter, and higher in frequency, which provides more detail to the exact location of the prey right before capture. The variation in these echolocation calls during the prey capturing process is split into two broad categories: frequency modulated (FM) calls with broadband components and constant frequency (CF) calls with narrowband components. Broadband FM pulses are characterized by short pulses that steeply sweep down frequencies, such as from 60 to 30 kHz within a few milliseconds in vespertilionids (Altringham 2011), or most South Carolina bat species. This steep sweeping or modulation is why they are referred to as frequency modulated calls, and they are used to detect nearby objects and are more accurate for localizing objects or prey. Narrowband CF calls are characterized by long pulses with a constant frequency, and are best used for detection of prey or objects further away. Because both calls are useful for different purposes, most bats use a combination of the two (Altringham 2011).

Different species of bats have a different acoustic structure to their echolocation calls, which can be a useful tool in the identification of a species (O'Farrell et al. 1999). However, the absolute frequency, harmonic structure, bandwidth, duration, and intensity all vary not only across species but also within them, which may occur due to different populations and habitat types (Neuweiler 1989, Fenton 1990, Barclay 1999). For example, in some species call features are distinct enough for the determination of that species to be fairly clear, but for other species there is too much overlap to tell. Recently however, there has been a shift from the focus on the time and frequency of calls for bat identification (referred to as zero-cross methodology) toward a technology that analyzes the full spectrum of the call in order to recognize additional characteristics specific to each species. This full-spectrum methodology is thought to increase robustness, accuracy, and confidence of identification. Specific bat detector and software programs are required depending on the methodology chosen to identify bat vocalizations. Recordings from both zero-cross and full-spectrum sampling require filtering and edits within bat identification software, and the calls identified may still need to be visually confirmed due to call similarities between species.

Foraging Behavior and Diet

Foraging Behavior

All of South Carolina's bats are insectivorous, and capture prey either during flight or by gleaning them from the surface of water, foliage, and even the ground (Hill and Smith 1984). Foraging bouts usually start in the first few hours after sunset, with activity slowing as individuals rest at night roots and increasing again a few hours before sunrise. However, emergence time and length of foraging bouts for adult females may differ depending on their reproductive stage and number of pups (Barclay 1989). Foraging behavior may include establishing foraging territories, as in the case of the hoary bat (Barclay 1984).

Foraging behavior varies within South Carolina bats, and is closely related to echolocation characteristics and morphology associated with each species. As previously mentioned, bats have differing acoustic structures within their echolocation calls. These echolocation characteristics are strongly related to differing foraging strategies: species that fly in cluttered habitats tend to use calls that quickly detect close objects, and species that fly in open habitats use calls that detect distant objects. To do this, lower intensity, shorter duration, higher peak frequency and a broader range of frequencies such as broadband FM calls are more often used by species that forage in dense vegetation. Higher intensity, longer duration, lower peak frequency with a narrower range of frequencies such as narrowband CF calls are more often used by bats that feed in more open areas (Schnitzler and Kalko 1998, Lacki et al. 2007). Additionally, species that glean insects off of foliage or the ground rely more on vision and hearing in order to detect their prey (Bell 1985, Faure and Barclay 1992).

Wing morphology characteristics are a major indicator of whether bat species tend to be slow and maneuverable in cluttered habitats with the ability to hover and glean insects from foliage, or perhaps specialize in fast flight and open-air hawking in uncluttered areas. These behaviors are often related to two major components of wing morphology: aspect ratio and wing loading. The aspect ratio (AR) can be calculated as the square of the wingspan length divided by the surface area of the wing (also calculated as the wing length divided the length of the fifth phalanx). A low aspect ratio generally indicates that a species has short, broad wings, which is often associated with bats that hunt insects among vegetation and have good maneuverability at low flight speeds (Norberg and Rayner 1987). On the other hand, a high aspect ratio generally indicates long, narrow wings, often associated with bats that prey on high-flying insects at high flight speeds (Norberg and Rayner 1987). Wing loading (WL) is determined by dividing the mass of the bat by its total wing area (also calculated by dividing the mass by the wing length times the length of the fifth phalanx). Low wing loading generally indicates a small bat with relatively large wings and slow flight, and high wing loading tends to indicate a large bat with relatively small wings and fast flight. However, these general statements are not always true as specific hunting patterns may vary over an evening. For example, little brown bats are known to initially feed along margins of lakes and streams and in and out of vegetation, and later in the evening forage over the surface of water in groups (Fenton and Bell 1979).

High WL is often found in combination with high AR, and indicates a fast, long-distance migrator that catches insects on the wing in open areas. Two species found in South Carolina that fit these characteristics are the Brazilian free-tailed bat and the hoary bat (Figure 5, colored in red). Even though the Brazilian free-tailed bat is a migrator in other portions of its range, it is a resident to South Carolina. In comparison, low WL and low AR indicate species with slow flight and high maneuverability that feed among vegetation and are generally known as clutter-adapted species. All of the *Myotis* species of South Carolina (eastern small-footed bat, little brown bat, northern long-eared bat, and southeastern bat), as well as the tricolored bat and Rafinesque's big-eared bat, tend to fall into this category (Figure 4, colored in green). Eastern red and Seminole bats have also been considered a clutter-adapted species, however, the activity of tricolored bats, eastern red bats, and Seminole bats did not differ above, within, or below the forest canopy in a South Carolina study by Menzel et al. (2005).

Two similar categories have species with somewhat long, pointy wings (though less so than the Brazilian free-tailed and hoary bats), and include the single *Lasionycteris* species and the rest of the *Lasiurus* found in South Carolina. These relatively pointy wings are good for either efficient flying in open areas, migration in more northerly portions of their range (though the majority in these categories are residents to South Carolina), or long-distance migration as in the case of the *Lasionycteris* species, or silver-haired bat. The faster flying category of these includes the northern yellow bat (Figure 5, colored in yellow), while the eastern red bat, Seminole bat, and silver-haired bat fly at relatively slower speeds (Figure 5, colored in blue). Many of these species are known to forage at or above treetop level, in open areas, over water, and in the case of the silver-haired bat, also along intact riparian areas and in or near coniferous and/or mixed deciduous forests (Kunz 1982*a*).

The big brown bat does not have particularly long or pointed wings, but is still considered a fast flier (Figure 5, colored in purple). This species has been known to forage among tree foliage instead of above or below the forest canopy (Schmidly 1991). Even though big brown bats have been recorded as flying above forest canopy in South Carolina (Menzel et al. 2005*b*), they are still readily captured below the canopy. The evening bat has intermediate wing shape and speed relative to other bat species in the state (Figure 5, colored in black), and despite its general classification as a clutter-adapted species, tends to forage above the forest canopy, in forest gaps, clear cuts, young tree stands, or over water in South Carolina(Menzel et al. 2001*a*, 2005*b*, M. A. Menzel et al. 2003).

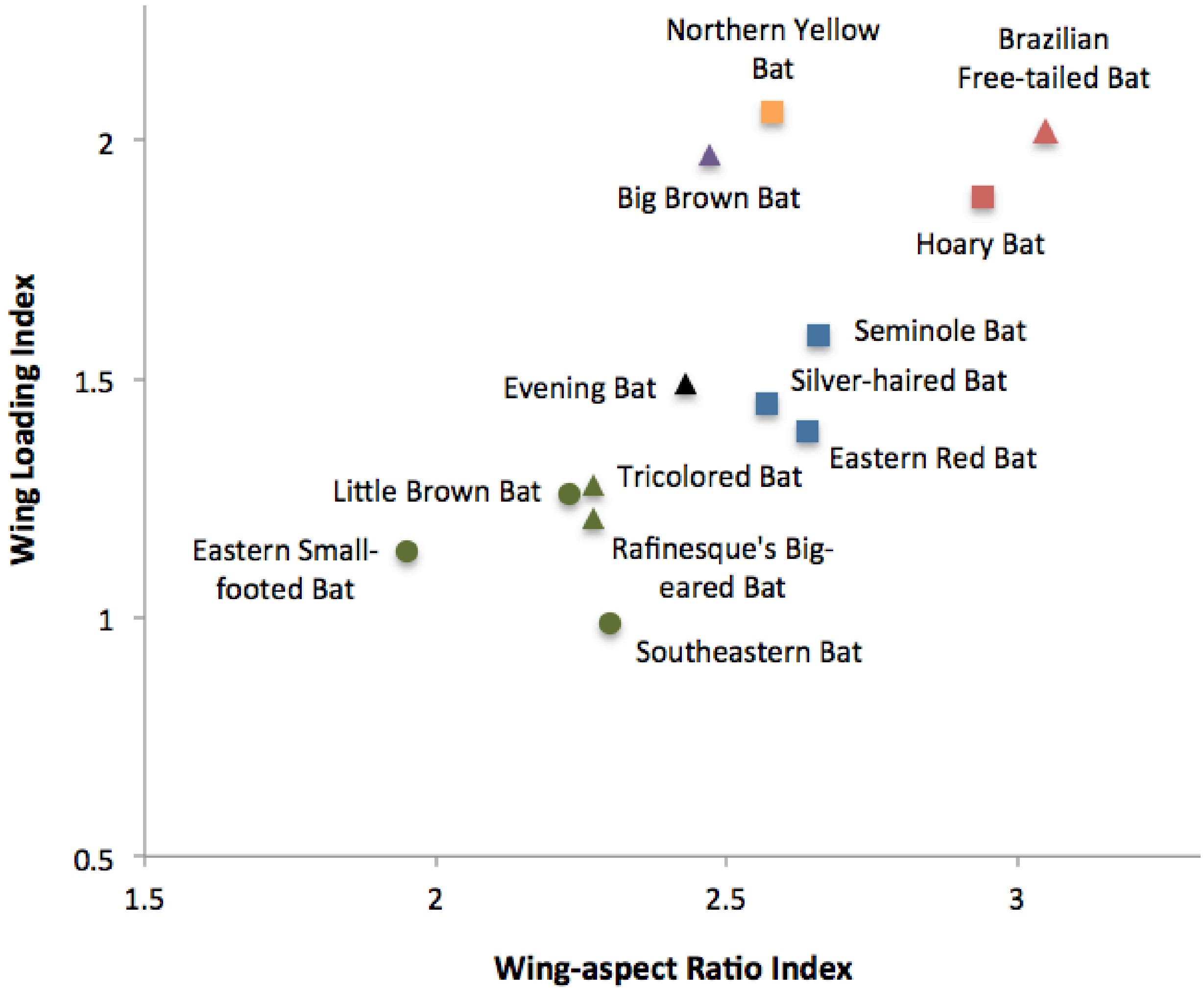

Figure 5: Wing loading and aspect ratios of southeastern bats. All calculations from bats captured at the Savannah River Site by M. A. Menzel et al. (2003) except eastern small-footed bat which came from Johnson et al. (2009). No information was provided for northern long-eared bat. Circles = colonial roosting *Myotis* species; Triangles = other colonial roosting species; Squares = foliage roosting *Lasiurus* and *Lasionycteris* species; Green = shortest, broadest wings and slowest speed; Red = longest, narrowest wings and fastest speed; Yellow = longer, narrower wings and faster speed; Blue = longer, narrower wings and slower speed; Purple = intermediate wing shape and faster speed; Black = intermediate wing shape and intermediate speed.

Diet

In the southeastern US, at least 12 dietary studies of bats have been conducted. Nearly half of those were in Florida (Sherman 1935, 1939, Jennings 1958, Zinn 1977, Zinn and Humphrey 1981), four in South Carolina (Armbruster 2003, Carter 1998/Carter et al. 2004, Donahue 1998, Menzel et al. 2002*a*), and two in Georgia (Carter et al. 1998, Menzel et al. 2000*b*). South Carolina's bats probably eat enough arthropods and insects to equal up to half or more of their body weight in one evening (Hill and Smith 1984, Kurta et al. 1989*a*, 1990, Kunz et al. 1995). Like most North American bats, the species found in the state are nearly all prey generalists and opportunistically feed on multiple insect orders (Lacki et al. 2007), though Rafinesque's big-eared bat shows moderate dietary specialization for Lepidoptera, and to a lesser extent so do hoary bats and the silver-haired bats. The top four most widely consumed prey groups of bat species known to occur in South Carolina are Lepidoptera, Coleoptera, Diptera, and Hymenoptera. The rest of the orders and suborders consumed by these species, along with examples of insect types within each, are listed in Table 3. However, diet studies in South Carolina have been conducted on only four species of bats, including the eastern red bat, evening bat, and Seminole bat (Carter 1998/Carter et al. 2004), as well as Rafinesque's big-eared bat (Armbruster 2003). Diet studies in the southeast have been conducted on four additional species, and include the tricolored bat, big brown bat, and northern yellow bat (Carter et al. 1998), as well as the southeastern bat (Zinn and Humphrey 1981). However, a recent PhD position with Clemson University will include research on stable isotopes and DNA analysis of bat fecal pellets in the eastern US.

Torpor

Torpor is a process whereby body temperature, oxygen consumption, and blood flow are reduced in a controlled manner in order to budget for periods of inactivity, and is an important life history strategy in bats (Altringham 2011). Bats may use daily torpor over a period of a few hours to conserve energy on a daily basis, and it is normally used in the active or warmer months of the year. The point at which torpor is considered hibernation is difficult to define, and depends on food, temperature and other demands. Generally however, hibernation is a deep torpor with greater declines in body temperature and metabolic rate for long periods of time such as days, weeks or months, and occurs seasonally in response to food reduction instead of declining temperatures (Geiser 2010, Altringham 2011). Bats do not remain in continuous torpor even during hibernation, and have the ability to wake spontaneously and independently of ambient temperature. Additionally, they may wake either spontaneously or from external factors. For example, little brown bats during summer torpor wake from stimulation of external factors, but while hibernating spontaneously arouse from torpor (Menaker 1961).

Bats save enormous amounts of energy with the use of torpor, either during unproductive foraging conditions or in habitats that would otherwise be too cold or harsh for survival (Bell et al. 1986, Chruszcz and Barclay 2002, Rambaldini and Brigham 2008). Some species, such as the eastern red bat, may become torpid at temperatures below 69°F (20°C) or 48°F (9°C) and survive subfreezing temperatures by maintaining body temperature just above the critical limit of 23°F (-5°C) (Reite and Davis 1966, Padgett and Rose 1991, Whitaker et al. 1997).

Table 3: Orders and suborders of insects consumed by bat species in South Carolina

Order or *Suborder*	**Insects**
Araneae	Spiders
Coleoptera	Beetles
Diptera	True flies, mosquitos, midges, gnats
Ephemeroptera	Mayflies
Hemiptera	True bugs
Heteroptera	Lygaeid bugs, waterbugs, bedbugs, stinkbugs, leaf-footed bug, shield bugs
Homoptera	Cicadas, aphids, leafhoppers, froghoppers, spittlebugs
Hymenoptera	Bees, ants, wasps
Isoptera	Termites
Lepidoptera	Moths, butterflies
Neuroptera	Lacewings
Orthoptera	Grasshoppers, crickets, locusts
Odonata	Dragonflies
Zygotera	Damselflies
Plecoptera	Stoneflies
Trichoptera	Caddisflies

Especially in the coastal regions, the mild winter conditions in South Carolina allow for many species of bats to use daily torpor and forage on warm nights when insects are available, and use intermittent, shallow hibernation only on particularly cold nights.

Daily torpor

The frequency of daily torpor varies depending on weather, food availability, season, sex, and reproductive condition, and is used by bats any time it's beneficial (Grinevitch et al. 1995, Geiser 2004, Klug and Barclay 2013). Additionally, the use of daily torpor may be used less by reproductive females than nonreproductive females and males. Reproductive females need to maintain high body temperature and speed the growth of the developing fetus (Kunz 1987, Kurta and Kunz 1988). However, these females may use torpor more often or for longer periods when pregnant than when nursing. This may be because the female isn't hindered by the weight of the fetus, and the fact that it is later in the year when warmer temperatures and higher food availability exist (Audet and Fenton 1988, Grinevitch et al. 1995, Chruszcz and Barclay 2002, Lausen and Barclay 2006, Willis 2006). Waking from daily torpor is energetically expensive, so males and nonreproductive females may seek cooler roosts during the morning to use deeper daily torpor more efficiently, and warmer roosts later in the day to assist in passive rewarming before arousing to forage in the evening (Hamilton and Barclay 1994, Willis 2006, Rambaldini and Brigham 2008).

Half of the bat species in South Carolina, including the northern long-eared bat which is considered a true hibernator, may wake from torpor to forage during warm winter nights. These include the big brown bat (Mumford

1958), Brazilian free-tailed bat (Barbour and Davis 1969, Lowery 1974, Wilkins 1989), eastern red bat (Padgett and Rose 1991, Whitaker et al. 1997), the northern long-eared bat (Whitaker and Rissler 1992*a*, Whitaker and Mumford 2009), northern yellow bat (Jennings 1958), Seminole bat (Wilkins 1987), and silver-haired bat (Humphrey 1975, Nagorsen and Brigham 1993, Dunbar 2007, Falxa 2007). Many of the other species in the state are known to be active year round and only enter torpor when the weather is extremely cold, such as Rafinesque's big-eared bat (Jones and Suttkus 1975, Ferrara and Leberg 2005). Also, Brazilian free-tailed bats may cluster together in groups to keep warm as the temperature decreases (Pagels 1975).

Hibernation

Hibernation usually lasts from three to seven months in North American bats, beginning around October and lasting through March or April. For species in South Carolina, the earliest bats to arrive at hibernacula and the last to leave are tricolored bats, who generally roost in hibernacula from late July through October and disperse in early April (Griffin 1940, Fujita and Kunz 1984, Schmidly 1991). At the other end of the spectrum is the eastern small-footed bat, which is one of the last to enter and one of the first to leave hibernacula, seldom entering before mid-November (Godin 1977, Gunier and Elder 1973,) and departing by early March (Mohr 1936).

Hibernation is generally entered with fat reserves of between 20 to 30 % of the body weight of the bat (Altringham 2011). This holds true for most hibernating bat species occurring in South Carolina except for the northern long-eared bat who is known to lose up to 45% of its body weight during winter in the northern portions of its range (Caire et al. 1979, Caceres and Barclay 2000). Additionally, female bats generally enter hibernacula at a higher weight than males (Ransome 1971). Bats may arouse from hibernation in order to seek suitable temperatures, avoid disturbance, enhance immune function, obtain water, mate, or forage outside the hibernacula (Ransome 1990, Thomas and Geiser 1997, Luis and Hudson 2006, Altringham 2011). Many species in North America often do not leave the hibernacula but resume torpor shortly after waking, which is true for obligate hibernators in South Carolina such as the tricolored bat (Whitaker and Rissler 1992*b*, Briggler and Prather 2003). This species also tends to stay in deep torpor for the longest periods of time than other temperate hibernating bats (maximum recorded at 11 days) (Twente et al. 1985, Amelon 2006).

Roosting Behavior

There are many important potential benefits provided by roosts for bats. These include protection from weather and predators, more efficient thermoregulation, shorter commuting distances to foraging sties, improved mating opportunities and maternal care, information transfer, and competition avoidance (Altringham 2011). Roosting behavior may differ depending on the abundance and dispersion of food, species, season, reproductive stage, sex, human disturbance, and proximity to foraging sites and water. Also, there are some common themes among bats and their roosts. For example, bats using stable roosts such as caves are frequently faithful to these sites over years and generations, and those that roost in foliage may have increased local movements but still be faithful to a particular location (Altringham 2011). There are four main types of roosts, categorized as day roosts, night roosts, maternity roosts, and hibernacula.

Day roosts and night roosts

A day roost is a roost used by bats during daylight hours where they spend the non-active part of the day resting or in torpor. Bat species occurring in South Carolina roost in a variety of structures typically including caves, mines, tunnels, rock crevices, tree foliage, beneath loose bark, tree cavities, buildings, bridges, and artificial bat roosts such as bat houses and bat towers. Species of bats in the *Lasiurus* genus, or the tree roosting bats, typically roost solitarily in tree foliage, tree cavities, and even Spanish moss in the case of the northern yellow bat and Seminole bat, but may also use woodpecker cavities (Fassler 1975), leaf litter (Moorman et al. 1999), dense grass (Mager and Nelson 2001), or grooves of palm trees (Davis 1974). Colonial roosting bats (including all *Myotis* species and others) typically roost in groups in caves, mines, tunnels, buildings, bridges, artificial roosts, and beneath tree bark, depending on the season and reproductive stage of the bat. As bats move between summer and winter roosts, short term day roosts may be referred to as a transient or interim roost, while migratory species moving between seasonal ranges may use migratory roosts.

A night roost is a temporary, short-term roost used by bats nocturnally to rest between foraging bouts, digest prey, escape predators, and find shelter from weather. These roosts are often associated with higher than ambient temperature, which is thought to aid in the conservation of energy as well as maintain higher metabolism needed for digestion (Buchler 1975, Fenton and Barclay 1980). Not much is known about night roosts used specifically in South Carolina. Elsewhere however, garages, breezeways, picnic shelters, and house porches are commonly used as night roosts for big brown bats (Harvey et al. 2011), ceilings of caves are used by eastern small-footed bats (Davis et al. 1965), different locations in the same buildings are used as day roosts by little brown bats (Barclay 1982), caves, mines, and quarry tunnels that differ from day roosts are used by northern long-eared bats (Jones et al. 1967, Clark et al. 1987), and caves, mines, and rock crevices are used by tricolored bats (Barbour and Davis 1969). Some species may not use night roosts at all if they tend to forage throughout the night, such as the Brazilian free-tailed bat (Whitaker and Hamilton 1998).

Maternity roosts

During spring and summer, most bats segregate by sex and reproductive status. Breeding females of foliage roosting bats generally rear young in tree foliage without a maternity colony, and colonial roosting bats gather in a maternity roost to rear young. Maternity roosts are often associated with higher than ambient temperature, which is thought to aid in maintaining higher metabolism needed for lactation and promoting fetal development and growth of the young. The temperatures required vary depending on species, but are usually between 70°F (21°C) and 90°F (32° C) (Tuttle and Taylor 1998). These warmer temperatures may be due to the location of the colony and/or the large numbers of individuals within the colony. The size of maternity colonies in South Carolina vary from five to a few hundred, and may be found in buildings, picnic shelters, attics, cavities of trees, under tree bark, and in artificial roosts. Maternity colonies of at least five species have been found in South Carolina, including big brown bats (Carter 1998, Menzel 1998), evening bats (Menzel et al. 2001*a*, Hein 2008), tricolored bats (Menzel et al. 1996), little brown bats (Loeb and O'Keefe 2006), and Rafinesque's big-eared bats (Bennett et al. 2003*b*, M. A. Menzel et al. 2003, National Park Service 2004). In the southeast, pup mortality events have been noted in big brown bats, and occasionally Brazilian free-tailed bats, in extremely hot weather in June or July.

Hibernacula and other winter roosts

Hibernacula are roosts used by bats during colder months such as in late fall, winter, and early spring. Bats enter torpor and hibernate during this time, and can survive by utilizing fat stores gained during the summer months. Types of hibernacula often occupied by bats in South Carolina include caves, mines, tunnels, rock crevices, buildings, and tree hollows. The temperatures within winter roosts are generally between 34°F (1°C) and 50°F (10°C), and hibernacula that have varying temperature regimes are beneficial to bats as it allows them to find suitable temperatures regardless of winter weather (Tuttle and Taylor 1998). However, bat species found in milder coastal areas may use hibernacula with temperatures of 59°F (15°C) or more (Webb et al. 1996). Besides temperature, humidity is an important factor in the selection of hibernacula. For example, little brown bats (Fenton 1970, Humphrey and Cope 1976, Nagorsen and Brigham 1993) and northern long-eared bats (Fitch and Shump 1979, Whitaker and Mumford 2009) are usually found in caves with high levels of humidity, sometimes from 70-95 %. High humidity is thought to help prevent dehydration in roosting bats since it reduces the amount of water lost to the air (Altringham 2011). Where there is information, many bat species in South Carolina hibernate singly or in small groups. The exceptions are the tricolored bat that is consistently found hibernating in groups of a few hundred individuals in South Carolina (but not in clusters, where individuals touch), and Rafinesque's big-eared bats that may hibernate together in clusters. For many species that hibernate in groups, males and females hibernate together. Hibernacula of at least seven species have been found in South Carolina, including the tricolored bat in abandoned mines and incomplete Blue Ridge Railroad tunnels in the mountains (Bunch et al. 2015*b*), little brown bats in caves and tunnels in Pickens County (Bunch et al. 2015*b*), eastern small-footed bats in a rock outcrop crevice in mature hardwoods in the mountains of Pickens County (Bunch and Dye 1999*a*), evening bats in Charleston County attics (M. A. Menzel et al. 2003), northern long-eared bats in a cave and single individuals in tunnels (Bunch et al. 1998*a*, Bunch 2011), Rafinesque's big-eared bats in a gold mine in Oconee County and abandoned buildings in Aiken County, and southeastern bats in cave system in Orangeburg County (J. M. Menzel et al. 2003).

Roost site fidelity and roost switching

Fidelity to roost sites depends on species-specific factors including sex, age, reproductive status, and social organization of bats, temporal factors such as season, and various environmental factors such as roost permanence and availability, disturbance, predation, parasites, and availability of food (Lewis 1995). For example, during summer some species may have high fidelity to maternal roosts, while during winter some may have high fidelity to hibernacula.

South Carolina bat species such as big brown bats (Davis 1967, Brenner 1968, Mills et al. 1975) have high fidelity to maternal roosts, and eastern small-footed bats (Gates et al. 1984), northern long-eared bats (Griffin 1945, Mills 1971, Caire et al. 1979), and tricolored bats (Hahn 1908, Menzel et al. 1999*a*) have high fidelity to hibernacula. Rafinesque's big-eared bats and foliage roosting bats such as eastern red bats and Seminole bats generally switch roosts frequently and do not have high fidelity to particular roosts, but may have high fidelity to certain areas or sites (Hutchinson 1998, Menzel et al. 1998, Mager and Nelson 2001). Frequent roost switching may be a response to changing microclimate conditions at different trees (Hoffmeister and Goodpaster 1963, McNab 1974, Jones and Suttkus 1975, Kunz 1982*b*). For example, roost switching is relatively rare for undisturbed Rafinesque's bats living in buildings (Clark 1990). For species with low fidelity to particular roosts but high site fidelity, stand and landscape features may be influence roost-site selection more than tree and plot characteristics (Lunney et al. 1988, Cryan et al. 2001, Elmore et al. 2004).

Movements and Migration

Nightly and seasonal movements

Most North American bats don't move long distances between day roost and foraging habitat (around 0.3 to 6 miles, or 0.5 to 10 km), and this holds true for many bat species that occur in South Carolina. Mostly in other states, distances from day roosts to foraging areas have been recorded at 0.62 to 1.24 miles (1 to 2 km) for big brown bats (Brigham 1991), 1,600 to 3,000 feet (500 to 900 m) for eastern red bats (Jackson 1961), 0.6 to 9 miles (1 to 14 km) for little brown bats (Henry et al. 2002), 2,000 feet (602 m) from maternity roosts for northern long-eared bats (Sasse and Pekins 1996), 358 feet (109 m) for a northern yellow bat (Krishon et al. 1997), and 0.62 miles (1 km) for Rafinesque's big-eared bats (Menzel et al. 2001*c*). The exception to short distances moved between day roost and foraging habitat is the Brazilian free-tailed bat that typically moves up to 50 miles (80 km) (Whitaker et al. 1980). For reproductive females, these distances may be shorter to more efficiently visit the maternity roost multiple times in a night.

Most bat species in South Carolina are considered nonmigratory, yet may have small seasonal movements. According to studies in other states, movement from summer roosts to hibernacula is less than 56 miles (90 km) in big brown bats (Mills et al. 1975, Neubaum et al. 2006), 0.06 to 0.68 miles (0.1 to 1.1 km) in eastern small-footed bats (Johnson and Gates 2008), 35 miles (56 km) in northern long-eared bats (Caire et al. 1979), 2.1 miles (3.4 km) in Rafinesque's big-eared bats (Finn 2000, Johnson and Lacki 2011), and 18 to 45 miles (29 to 72 km) in southeastern bats (Rice 1957). Some species, such as the Brazilian free-tailed bat, eastern red bat, hoary bat, and tricolored bat are migratory in the northern portions of their range, but are generally considered year round residents to South Carolina (M. A. Menzel et al. 2003). In the past, a Brazilian free-tailed bat colony was known to roost in an old church the Piedmont region of South Carolina during summer, but leave for the winter to an unknown location. The majority of hoary bats in South Carolina probably migrate north in spring as they are rare in the state during summer, but there is evidence that some are found here during that time (M. A. Menzel et al. 2003). For species such as the northern yellow bat, it is suspected but unknown if they are resident to the state.

Migrational movements

Long-distance migrants are known to move hundreds of miles across the continent, and long-distance migrants that occur in South Carolina are the hoary bat and the silver-haired bat (Cryan 2003). As mentioned above, the hoary bat may be resident to the state. However, silver-haired bats are migratory to South Carolina as they are over much of their range. This is thought to shift to the north in the spring and to the south in the fall, though the southern shift appears to be more extensive in eastern than western North America (Baker 1978, Izor 1979). Females migrate further than males, and males are only present throughout the range during migration (Kunz 1982*a*). The timing of fall migration for this species generally occurs in two waves, primarily from August through September (Barclay 1984, Arnett et al. 2008, McGuire et al. 2012). In eastern North America, McGuire et al. (2012) predicted the fall migration rate of silver-haired bats from the north side of Lake Erie to the southeastern US be 155 to 170 miles (250 to 275 km) per night for five to six nights without refueling, even though brief stopovers of one to two days do occur. However, migrating individuals do engage in feeding activity, especially on non-travel nights (Reimer et al. 2010, McGuire et al. 2012). Spring migration also happens in waves, and occurs along the southern shore of Lake Manitoba in May and early June (Barclay et al. 1988). In South Carolina, silver-haired bats are distributed statewide, but during summer they are not generally found in the lower Piedmont or Coastal Plain due to their migratory patterns (M. A. Menzel et al. 2003, Bunch et al. 2015*a*), but are found in the northwest corner of the state in April and July (Webster 2013).

Little brown bats could be considered migratory because they may migrate several hundred miles between hibernacula and summer roosts in other states (Davis and Hitchcock 1965, Fenton 1970, Humphrey and Cope 1976), especially in the northeast (Schmidly 1991). However, it is unknown where most of South Carolina's summer populations of little brown bats spend the winter or how far they migrate (Bunch et al. 2015*b*).

Habitat Requirements

Roosting Habitat

Roosting habitat is extremely important in the daily lives of bats as they spend most of their lives in roosts. As mentioned in the section on roosting behavior, categories of roosts include day roosts, night roosts, maternity roosts, and hibernacula. Within each of these categories are specific types such as caves and mines, rock crevices, buildings, bridges, trees, and artificial bat roosts that will be covered in detail in this section. Types of roosting habitats used by bat species occurring in South Carolina can be found in Table 4.

Understanding how and where bats roost provides key facts about their distribution, densities, seasonal movements, social structure, and foraging and mating strategies. Knowing which roosts bats have high fidelity to is important conservation information, since these sites are critical for raising young, maintaining social contacts, and offering suitable conditions for hibernation (Kunz 1982*b*, Lewis 1995). Roost selection research has provided useful information for small-scale characteristics of bat roosts, but it is important to keep in mind that for many bat species such as tree roosting bats, stand and landscape scales may be of equal or greater importance (Lunney et al. 1988, Cryan et al. 2001, Elmore et al. 2004, Miles et al. 2006). Additionally, it is possible that roost sites selected may differ based on landscape conditions. For example, day roosts selected in Georgia on a natural site were based on tree, plot, and landscape characteristics, but on the managed site they were selected at the tree and plot scale (Miles et al. 2006). In this case, less roosting structures over the landscape were probably available due to the young forest stand age of the managed areas. Finally, other potentially limiting landscape

Table 4: Roost types used by bat species known to occur in South Carolina. Modified from Menzel et al. (2003).

	Roost Type							
Common Name	Cave or Mine	Foliage	Spanish Moss	Tree Bark or Cavity	Cliffs, Talus, or Rock Crevices	Artificial Structure	Bird/Squirrel Nest	Leaf Litter
Big Brown Bat	WS			WS	S*	WS	S*	
Brazilian Free-tailed Bat				W* S*		WS		
Eastern Red Bat		WS	WS*	S*		S	W* S*	W
Eastern Small-footed Bat	WS*			S*	S	S		
Evening Bat		S	S*	S		WS		
Hoary Bat		WS	W*	W* S*			W*	
Little Brown Bat	WS			S	S*	S		
Northern Long-eared Bat	WS*			S	W*	WS		
Northern Yellow Bat		WS	WS					
Rafinesque's Big-eared Bat	WS			WS	WS	WS		
Seminole Bat		WS	WS	WS				W
Silver-haired Bat	W	S*		WS	W* S	W	S*	
Southeastern Bat	WS			WS		WS		
Tricolored Bat	WS	S		S		WS		

W = winter roost; S = summer roost; * = Not necessarily observed/common in South Carolina, but possible

features like nearby foraging areas and water resources may also play a part in roost selection by bats.

Caves, mines, and tunnels

Caves and mines are the most stable and persistent roosts, and the most often used during winter for hibernation. Otherwise, they may be used as night roosts, transient roosts, or a place to raise young (Barbour and Davis 1969, van Zyll de Jong 1985). Nine of the 14 species in South Carolina use caves, mines, or tunnels at some point during the year (Table 4). Tricolored bats are often the largest populations of bats found in these types of roosts in the state (Bunch et al. 2015*b*).

For a cave or mine to be suitable for bats, the microclimate needs to have just the right conditions for the differing stages of a bat's life cycle (Tuttle and Taylor 1998). Airflow, air temperature, and humidity are environmental factors important to suitable cave site selection, which are influenced by the season as well as the size, configuration, and complexity of the cave (Tuttle and Taylor 1998, Sherwin et al. 2009, Altringham 2011). However, there are only two well-known caves in South Carolina, one located in the Blue Ridge region and the other in Orangeburg County in the Coastal Plain.

Because South Carolina doesn't have many caves, similar roosts such as mines, abandoned tunnels, and old bunkers are especially important to bats in the state. Over 200 known or potential mine locations have been mapped by SCDNR, most of which are mines or prospects in the Piedmont region that were placer mines with no adits or shafts, and thus provided no underground bat roosts. However, of the 58 surveyed that had potential for bat roosts, nine had an underground component with tricolored bats present. South Carolina also harbors abandoned tunnels in the Blue Ridge region and old bunkers in the Piedmont region. Two major hibernacula for tricolored bats exist in the incomplete Blue Ridge Railroad tunnels. The Stumphouse Mountain Tunnel is owned by Clemson University and managed by the city of Walhalla, and the Middle Tunnel has a bat friendly entrance gate and is owned and managed by SCDNR as part of the Stumphouse Mountain Heritage Preserve. Six World War II bunkers at SCARNG McCrady Training Center near Columbia, SC provide important hibernacula and roosting habitat for various bat species in the state including big brown bats and Rafinesque's big-eared bats.

Cliffs, talus, and rock crevices

Cliffs, talus or rock crevices may be used during various seasons by bat species in South Carolina. The bat species commonly known to use these roosts are eastern small-footed bats and Rafinesque's big-eared bats, though big brown bats, little brown bats, northern long-eared bats, and silver-haired bats may also do so occasionally (Table 4). Rafinesque's big-eared bats have been found in a rock cliff area on Duke Energy owned property at the Bad Creek, Whitewater River research area (J. M. Menzel et al. 2003). Factors important to selection by bats of suitable sites include protection from predators, temperature, and proximity to water sources and foraging areas, though rock crevices rarely offer the same protection or thermal stability as caves (Rancourt et al. 2005, Altringham 2011). However, very little research has been conducted on these types of roost sites due to the difficulty of detecting bats within them. Species that use these sites often roost singly or in small groups, tuck themselves deeply within crevices, and, as in the case of eastern small-footed bats, are also very small.

Buildings and bridges

Buildings and bridges may be used as hibernacula, maternity roosts, and substitutes for other natural roost types used in the past. In fact, a few bat species have benefited from these types of artificial roosts through populations increases and growing distributions (Kunz and Reynolds 2004). For example, buildings are considered the most important hibernacula for big brown bats in northwestern US (Nagorsen and Brigham 1993, Maser 1998).

Buildings used by bats commonly include houses, garages, barns, churches, cabins, and picnic shelters, and may be used as day roosts, night roosts, maternity roosts, or hibernacula. They may either roost inside, such as in an attic or a chimney, or on external portions of a building such as underneath wooden shingles, shutters, wooden siding, eves and porches. The gaps in a building's exterior don't need to be very large for a bat to enter, and can be as narrow as 0.4 inches (9.5 mm) or a hole as small as 0.7 inches (1.8 cm) across (Greenhall 1982). Older or abandoned buildings with many entry points are often a preferred roost, especially when coupled with the lack of human disturbance. Bat species in South Carolina most commonly found in buildings are the big brown bat, Brazilian free-tailed bat, evening bat, and tricolored bat. Less commonly found are little brown bats in buildings and picnic shelters at the SCDNR Fish Hatchery in Oconee County (Bunch et al. 2015*b*), and eastern small-footed bats in a woodpile on a porch, a fish hatchery building, a picnic shelter, and under loose tarpaper of an abandoned log cabin (Bunch and Dye 1999*a*, Bunch et al. 2015*b*). Eastern red bats are sometimes found in shingles of houses, and evening bats, northern long-eared bats, and silver-haired bats are thought to use houses as winter roosts. Maternity colonies of evening bats, northern long-eared bats, Rafinesque's big-eared bats, and southeastern bats could be found in buildings as well.

Bridges, especially large concrete ones, may be used as day roosts, night roosts, maternity roosts, or hibernacula (Keeley and Tuttle 1999). Wooden and metal bridges without concrete joints don't seem to be used as often as concrete bridges, potentially because of the less stable thermal environment of metal bridges or the pungent odor caused by creosote that often coats wooden bridges. Concrete bridges provide a more thermally stable environment, as during the day they provide cooler temperatures and at night provide warmer temperatures than ambient air (Keeley and Tuttle 1999). Usually, locations on bridges used by bats are in expansion joints, corners located between beams, and other crevices. Bat species in South Carolina that use bridges include big brown bats, Brazilian free-tailed bats, eastern small-footed bats, Rafinesque's big-eared bats, southeastern bats and tricolored bats. All of these species except tricolored bats are known to use bridges as maternity roosts, though big brown bats, Rafinesque's big-eared bats, and southeastern bats may also use bridges as winter roosts. In a South Carolina study by Bennett et al. (2008) from May to August, Rafinesque's big-eared bats selected large, concrete T-beam and I-beam girder bridges as day roosts and avoided flat-bottomed slab bridges. These were used as either solitary or maternity roosts, though most of the occupied bridges were in the Upper and Lower Coastal Plains, with a few in the Piedmont region, and none in the Blue Ridge region.

Trees

Nine of the 14 bat species in South Carolina use trees for roosting during multiple seasons, and nearly all are known to use tree roosting sites at some point during the year (Table 4). Tree roosting sites may exist in the form of tree crevices, cavities, foliage, Spanish moss, palm fronds, squirrel nests, or woodpecker cavities. Overall, many bat species in North America are known to select for higher roosts in larger trees within more open canopy and higher snag density (Menzel et al. 1998, Kalcounis-Ruppell et al. 2005), which may provide benefits such as easier roost access, protection from predators, and increased solar exposure for the growth of young (Racey and Swift 1981, Racey 1988, Vonhof and Barclay 1996). However, colonial cavity roosting bats tend to prefer more open canopies and be closer to water than foliage roosting bats (Kalcounis-Ruppell et al. 2005). The tree species chosen for roosts only seem to matter to bats when it comes to the characteristics and extent of decay that occur in that tree species. Factors of decay that provide suitable roost sites include the presence and amount of loose bark, trunk furrows, and either natural cavities or those constructed by woodpeckers. Additionally, early stages of decay may be selected for over rotten wood since more bark is generally retained and firm wood provides more effective insulation (Crampton and Barclay 1998). Since woodpeckers are the primary excavators of cavities used by bats, and these cavities are used by species such as the little brown bat, silver-haired bat, and big brown bat, understanding the abundance and excavation preference of woodpeckers and ultimately assist in bat conservation (Kalcounis and Hecker 1996, Mattson et al. 1996, Vonhof and Barclay 1996, Kalcounis and Brigham 1998). Generally, trees with decayed heartwood and relatively hard sapwood are preferred by woodpeckers (Harestad and Keisker 1989). Forest age and structure play an important role for many bats since they commonly roost in forests with higher snag densities and higher snag or live tree basal areas (Campbell et al. 1996, Cryan et al. 2001, Kalcounis-Ruppell et al. 2005). The closer tree roosts are to foraging and drinking areas, the less energy bats have to spend commuting. However, Barclay and Kurta (2007) found that access to other resources was not as important as the availability of suitable roost trees. The number of trees used by bats in eastern North America has been reported as one to six per bat and eight to 25 per colony for maternity colonies (Barclay and Kurta 2007).

Colonial roosting bats in the state are often found roosting under tree bark, using cavities, and may even be found in the foliage of trees as in the case of the tricolored bat during summer. Though big brown bats historically used loose bark and cavities of pine, oak, beech, bald cypress and other tree species, they now generally roost in human-made structures. However, in South Carolina they have been found using a hollow bald cypress for a maternity colony in a bottomland hardwood swamp (Carter 1998, Menzel 1998). Colony size of this species may depend on tree roost size as larger cavities of roost trees have been found to be correlated with larger numbers of reproductive female big brown bats (Willis et al. 2006). Brazilian free-tailed bats historically used the hollows of mangroves and cypress trees in the southeast (Jennings 1958), but like big brown bats, mainly use human-made structures today. Evening bats roost in hollow trees and under loose bark (Barbour and Davis 1969, Chapman and Chapman 1990, Menzel et al. 2001*a*), and have also been found in Spanish moss (Jennings 1958) and underneath palm fronds (Taylor and Lehman 1997). At the Savannah River Site in South Carolina, roosts were in cavities or under exfoliating bark and most commonly in longleaf pines (*Pinus palustris*), though conifer snags in beaver ponds were also common (Menzel et al. 2000*a*). In this study, compared to random plots, roosts were found in areas with taller and less dense canopy, greater snag abundance, the overstory had less trees and lower richness, and the understory had less trees, lower richness and lower diversity. In the lower Coastal Plain of South Carolina, evening bats roosted in cavities in hardwood trees and fork-topped loblolly pines (*Pinus taeda*), selecting roost sites in mixed-pine hardwoods (Hein 2008). Additionally, about 40% of male and 20% of female roosts were located in forested corridor stands. Evening bat maternity colonies in South Carolina used mature longleaf pine stands with a higher overstory, greater canopy density, and greater proportion of basal area composed of conifers compared to roosts used by solitary evening bats surrounding the maternity colony (Menzel et al. 2001*a*). Of the 33 maternity colonies found in the state by Hein (2008), 15 smaller colonies were in fork-topped trees and 18 larger colonies were found in tree cavities. Tricolored bats are known to utilize trees (Humphrey 1975) and squirrel nests (Veilleux et al. 2003) for maternity roosts. Veilleux et al. (2003) found that 19 reproductive tricolored bats in Indiana preferred oaks as roost trees, and roosted exclusively in foliage, with 65% in clusters of dead leaves, 30% in live foliage, and 5% in squirrel nests. In this study, they also found the mean roost tree height to be around 68 feet (20.8 m), the roost height from the ground to be 52 feet (15.7 m), and the roost tree diameter at breast height to be 13 inches (33.2 cm). Male tricolored bats in North Carolina are known to use large diameter oaks and hickories for roosts (Bunch et al. 2015*b*). In South Carolina, this species has been found in the cavities of bottomland hardwood tree species such as swamp chestnut oak (*Quercus michauxii*), sweetgum, and laurel oak (*Q. laurifolia*) (Carter et al. 1999), as well as in Spanish moss in understory trees on exposed high-marsh hammocks (Menzel et al. 1999*a*). Female tricolored bats often form maternity colonies of three to five individuals in clusters of live or dead leaves in trees, but basal cavities may also serve as maternity roosts (Menzel et al. 1996).

All *Myotis* species in South Carolina are colonial roosting bats, and include the eastern small-footed bat, little brown bat, northern long-eared bat, and southeastern bat. These species use roosts in tree cavities or under loose bark either during winter, summer, or both (Table 4). Eastern small-footed bats usually roost in human-made structures, caves, or mines, but are sometimes found beneath the bark of trees during summer (Barbour and Davis 1969). For little brown bats, maternity sites may be located in human-made structures, bat boxes, hollow trees, and taller, larger diameter trees in older forest habitat are commonly selected by tree-roosting reproductive females (Kalcounis and Hecker 1996, Crampton and Barclay 1998). Northern long-eared bats roost in tree cavities (Owen et al. 2001, Menzel et al. 2002*d*) and under the bark of trees (Mumford and Cope 1964). According to the USFWS (2015*b*), potential suitable summer habitat for northern long-eared bats may include live trees and/or snags with a dbh greater than or equal to 3 inches (7.62 cm) that have cavities, crevices, exfoliating bark, and/or cracks, and individual trees are within 1,000 feet (305 m) of forested habitat. In addition, wooded corridors and human-made structures should also be considered potential suitable summer habitat. Maternity colonies of this species have been found in trees, tree cavities, and under bark (Foster and Kurta 1999, Caceres and Barclay 2000, Whitaker and Mumford 2009). Many (though not all) studies show that female northern long-eared bats in maternity colonies prefer roosts in tall hardwood trees in early stages of decay (Sasse and Pekins 1996, Caceres 1998), in live trees with less canopy closure (Caceres 1998), and in large diameter trees (Sasse and Pekins 1996, Foster and Kurta 1999). In South Carolina during summer, a lactating northern long-eared bat was tracked to a location under the loose bark of a dead pine near National Forest land in Oconee County (Bunch and Dye 1999*b*).

Two bat species that most commonly utilize tree species associated with the bottomland hardwood forests of the Coastal Plain in South Carolina are the southeastern bat and Rafinesque's big-eared bat. Southeastern bats use various bottomland hardwood tree species such as large, live, hollow black gum and water tupelo with large basal openings (Cochran 1999, Hoffman 1999, Carver and Ashley 2008), sweetgum (*Liquidambar styraciflua*), Nuttall oak (*Q. nuttallii*), water hickory (*Carya aquatica*), water oak, red maple (*Acer rubrum*), American sycamore (*Platanus occidentalis*), American beech (*Fagus grandifolia*), bald cypress, Pignut hickory (*C. glabra*), swamp chestnut oak (*Q. michauxii*), and overcup oak (*Q. lyrata*) (Reed 2004, Wilf 2004, Stevenson 2008, BCI and SBDN 2013, Bat Conservation International 2015). During summer, this species prefers larger trees with larger cavities within 66 feet (20 m) of standing water (Mirowsky 1998), and the diameter at breast height of roost trees are often large, varying from 30 to 61 inches (76 to 155 cm) (BCI and SBDN 2013). In South Carolina, live tupelo gum trees within closed canopies were the primary roosting site for the southeastern bat in the Francis Beidler Forest (Clark et al. 1998). Despite being available, large bald cypress trees were not used as roost sites in the Francis Beidler Forest or in areas in Texas, even though they are used as roost sites in Mississippi (Clark et al. 1998, Mirowsky 1998, Stevenson 2008). Southeastern bats also roost in trees in winter, especially in southern regions. In Florida, they move from caves that are too warm to facilitate torpor to exposed roosts in tree hollows and human-made structures (Rice 1957, Humphrey 1992). Also, one study found this species may prefer larger trees with larger cavities during winter than spring and summer (Fleming et al. 2013). Rafinesque's big-eared bats are often found in roosts in hollow trees (Trousdale and Beckett 2005, Trousdale 2011), and sometimes found in tree crevices (Lance 1999) and beneath loose bark (Handley 1959). In South Carolina, they have been found in human-made roost towers in the Blue Ridge and Piedmont regions (Greenville and Pickens Counties), the Sandhills region (Aiken and Richland

Counties), and in the Coastal Plain (Hampton County). Roost trees usually stand 59 to 82 feet (18 to 25 m) tall, have large cavities greater than 3.6 feet (102 cm) tall and 1.3 feet (39 cm) wide, and tend to be near water (Mirowsky 1998, Gooding and Langford 2004, Trousdale and Beckett 2005, Carver and Ashley 2008). However, Loeb and Zarnoch (2011) found that anthropogenic roosts used by the Coastal Plains and Sandhill populations (those of *C. r. macrotis*) were used significantly more than tree roosts during summer. Mountain populations (those of *C. r. rafinesquii*) in summer use roosts in cavity trees such as tulip poplars (*Liriodendron tulipifera*) (Bunch et al. 1998). Nursery colonies may form on vertical surfaces inside trees (Carver and Ashley 2008, Stevenson 2008). Also, roost tree density affects the social structure of Rafinesque's big-eared bats, where lower densities may lead to the use of only one focal maternity roost (Johnson et al. 2012). In South Carolina, maternity colonies have been found in tree cavities with approximately 100 individuals at Congaree National Park (National Park Service 2004). In the southern Coastal Plain where caves, mines, or other karst features are unavailable during winter, this species may remain in large hollow trees of closed canopy bottomland hardwood forests. Rafinesque's big-eared bats may choose larger diameter trees in winter than in spring and summer, as they've been known to do in the bottomland hardwood forests of Mississippi (Fleming et al. 2013).

Foliage roosting bats such as eastern red bats, hoary bats, northern yellow bats, Seminole bats, and silver-haired bats are highly dependent on trees for roosts throughout their life cycle. Stand and landscape features may be more influential for roost-site selection than tree and plot characteristics for these species as they often have high fidelity to specific sites despite switching tree roosts often within those sites (Lunney et al. 1988, Cryan et al. 2001, Elmore et al. 2004). Eastern red bats are found roosting on leaf petioles and small branches in the tops of deciduous trees in summer (Barbour and Davis 1969). In central Illinois, Mager and Nelson (2001) found 89 % of roosts were in foliage or the trunks of deciduous trees greater than 18 inches (45 cm) dbh. Though eastern red bats are often found roosting in deciduous trees, Elmore et al. (2004) found that within thinned pine stands of Mississippi, 70% of their day roosts were found in 16 species of hardwood trees and 30% in loblolly pines. Also, preferred roosts were located within denser subcanopy and higher basal area, but specific tree characteristics were not as important as those at the stand-level. At the Savannah River Site, eastern red bat roosts were found in 23 total tree species, with sweetgum (*Liquidambar styraciflua*) and red maple (*Acer rubrum*) used most (Menzel et al. 2000*a*). In the same study, roost trees were found in stands with larger basal areas, higher and denser overstory, and more diverse overstory and understory. In the Clemson Experimental Forest in South Carolina, female eastern red bats have been found to select trees on north and northwest facing slopes (Leput 2004), and roosts in Georgia and South Carolina forests were found at an average height of 50 feet (15.3 m) (Menzel et al. 1998). Though winter habits of eastern red bats are not well known in the state, they are found feeding throughout the year in southeastern Virginia and northeastern North Carolina at temperatures above 48°F (9°C) (Padgett and Rose 1991, Whitaker et al. 1997), and may hibernate in leaf clusters, tree branches, woodpecker cavities, old squirrel nests, leaf litter, and Spanish moss during colder winter temperatures (Constantine 1958, Barbour and Davis 1969, Fassler 1975, Saugey et al. 1989). Hoary bats have been known to roost in trees such as elm (*Ulmus* species), black cherry (*Prunus serotina*), plum

(*Prunus* species), box elder (*Acer negundo*), and osage orange trees (*Maclura pomifera*) at about 10 to 16 feet (3 to 5 m) above the ground (Shump and Shump 1982*a*). Day roosts used by this species are almost exclusively in the foliage of trees (Shump and Shump 1982*a*, Willis and Brigham 2005). Hoary bats may also use tree cavities, Spanish moss, and old squirrel nests, especially during winter (Neill 1952, Cowan and Guiguet 1965, Constantine 1966). Northern yellow bats have been found roosting in Spanish moss in live oaks (*Quercus virginiana*) in Georgia and Florida (Jennings 1958, Menzel et al. 1995, Coleman et al. 2012), in pine-oak woodlands in Florida and Mexico (Sherman 1944, Jones 1964, Carter and Jones 1978), in the grooves of palm trees in Texas (Davis 1974), and on the stems of hardwoods in Virginia (Rageot 1955). Seminole bats commonly roost in oak hammock communities in Spanish moss from fall through spring and even during winter (Constantine 1958, Jennings 1958, Barbour and Davis 1969), but also in the canopy of live pine trees (Menzel et al. 1998, 1999*a*, 2000*a*, Perry and Thill 2007*a*) and sometimes roost under loose bark in the summer (Sealander 1979). Roost sites for this species often have west and southwest exposures that are thought to provide warmth from the sun (Constantine 1958, Wilkins 1987). Seminole bats may roost at heights great enough for the bat to drop into unobstructed space in order to take flight and vary from 3.6 to 14.8 feet (1.1 to 4.5 m), but may roost closer to the forest floor during colder weather (Constantine 1958). In South Carolina, this species may also roost in the terminal branches of pine limbs in pine dominated communities (Menzel et al. 1998), and at the Savannah River Site roosts were primarily located in loblolly pines (*Pinus taeda*) (Menzel et al. 2000*a*). In the latter study, roosts tended to be in taller, larger trees found in areas with higher basal area, lower species richness understory, and less Spanish moss than neighboring trees. Silver-haired bats have shown a roosting preference for forests with large numbers of snags (Campbell et al. 1996, Mattson et al. 1996, Betts 1998) and old-growth forests (Thomas 1988, Jung et al. 1999). During summer, roosts and nursery sites for this species are often found in tree foliage, under loose bark, in narrow crevices in tree trunks, or in old woodpecker cavities (Parsons et al. 1986, Betts 1996, Mattson et al. 1996, Vonhof and Barclay 1996). In Washington, roosts included dead or dying trees with exfoliating bark, extensive vertical cracks, or cavities, and were significantly taller than surrounding trees with less overstory, less understory, and shorter understory vegetation than comparable random plots, and the height of summer roosts ranged between 20 to 50 feet (6.1 to 15.2 m) (Campbell et al. 1996). Maternity roosts for silver-haired bats are usually found in old woodpecker cavities (Parsons et al. 1986, Mattson et al. 1996, Vonhof and Barclay 1996) and in taller trees with retained tops protruding above the canopy (Betts 1998), possibly in order to better absorb sunlight and retain heat. Day roosts of males and non-reproductive females have been found in cavities as well as under loose bark on large trees in intermediate stages of decay (Mattson et al. 1996). During late summer and early fall, migrating silver-haired bats have been known to roost in narrow crevices in tree trunks at heights of 2.9 to 11.5 feet (0.87 to 3.5 m) with significantly larger circumferences than random samples (Barclay et al. 1988). In Arkansas, Perry et al. (2010) found that 90% of winter roosts were in five species of trees, and most were on southern topographic aspects. Of all roosts, 55% were under loose bark and 6% were either under a tree roost or in a cavity at the base of a live pine. Pine or pine-hardwood stands greater than 50 years old and used forest stands between 15 and 50 years old were selected as winter roosts by silver-haired bats in this study.

Artificial bat roosts

Typical bat boxes, multi-chamber nursery boxes, and structures that mimic large hollow trees such as large bat towers are all examples of artificial bat roosts used by colonial roosting bats in South Carolina. Almost any bat that roosts in buildings or under bridges is a candidate for the use of various bat boxes. However, certain species may require specific types of bat boxes. For example, typical bat boxes are best used for big brown bats (and potentially Brazilian free-tailed bats, evening bats, silver-haired bats, and tricolored bats) (Tuttle et al. 2005). Multi-chamber nursery boxes are best used for eastern small-footed bat, little brown bat, and northern long-eared bat colonies, and bat towers are best used for Rafinesque's big-eared bats and southeastern bats.

For an artificial roost to be successfully used by bats, it is important to determine the correct placement, design, and construction for target bat species (Kiser and Kiser 2004). For example, artificial roosts should have a south, east, or west facing aspect for better heat absorption (Mering and Chambers 2014). Additionally, understanding local, natural bat populations before providing artificial roosts will help prevent unintentional negative impacts on the species composition of those populations. For example, providing artificial roosts was shown to increase the population of a dominant bat and caused a forest bat that did not use artificial roosts to become increasingly rare (Bender 2005). A way to prevent this may be to create alternative roosts that closely mimic the natural roosts of target species in design, height, and microclimate (Mering and Chambers 2014). Alternative roost sites are useful for bats evicted from buildings or other human-made structures; yet they should not generally be considered an effective mitigation measure for replacing natural roost sites. However, they can be used in forests as supplemental bat roosts (Mering and Chambers 2012). There are many online resources for the purchase of bat boxes as well as how to construct them, such as BCI's "The Bat House Builder's Handbook" (Tuttle et al. 2005).

Bat boxes have been set up at South Carolina state parks such as Oconee State Park and Table Rock State Park, which have seen use by little brown and big brown bats. Also, when bat boxes have been provided during exclusion from nearby structures, big brown bats and Brazilian free-tailed bats have been known to move to those bat boxes. However, there is still room for improvement in bat box design in the southeast because extreme heat can cause bats to hang out of the bottom of the box and potentially drop pups on the ground. In terms of bat towers in South Carolina, one or more Rafinesque's big-eared bats have made use of five out of seven set up across the state thus far, located in the Blue Ridge and Piedmont regions (Greenville and Pickens Counties), the Sandhills region (Aiken and Richland Counties), and in the Coastal Plain (Hampton County).

Foraging and Commuting Habitat

Of the 18 bat species that occur in the southeast, all rely on forests for foraging habitat (Hall 1981). Habitats used during foraging bouts by bats in South Carolina are extremely variable, covering most habitat types available except offshore marine waters. These habitats range from wetlands and riparian areas, bottomland hardwoods such as bald cypress-tupelo gum swamps and beech-magnolia bottoms, coastal prairies, hammocks, Carolina bays, loblolly-slash pine habitats, pine savannahs, pine barrens, oak habitats, open grasslands, agricultural lands and floodplains, mixed and mature deciduous uplands, edges of clearcuts, golf courses, airports, and rural and urban areas. Within these habitats, bats may feed over streams, ponds and lakes, along cliff faces, in the forest canopy or understory, in unfragmented forest, or in forest openings. Most foraging activity generally occurs along edge habitats or in open sites such as golf courses, fields, clearcuts, and forest gaps, potentially because these areas are where the highest concentrations of insects are most easily consumed compared to areas of vegetational clutter found in interior forest habitat. However, species such as Rafinesque's big-eared bats are known to avoid large open areas (Clark 1990, 1991), and according to Menzel et al. (2001), big brown bats in the southeast may prefer hardwood and pine forests over agricultural fields and clear cuts. As mentioned in the Foraging Behavior section of this document, wing loading, wing aspect, and echolocation characteristics of bats play a significant role in what habitats they are best able to exploit. For example, the high wing loading and aspect ratio of Brazilian free-tailed bats and hoary bats indicate fast, long-distance migrators that catch insects on the wing in open areas. Foraging habitats may also vary over an evening for some species. For example, little brown bats initially feed along margins of lakes and streams and in and out of vegetation 7 to 16 feet (2 to 5 m) above the ground, and later forage 3 to 7 feet (1 to 2 m) over the surface of water in groups (Fenton and Bell 1979).

Water

Many species of bats in South Carolina incorporate water in their foraging areas, whether it is over, adjacent to, or along margins of bodies of water, wetlands, riparian areas, or bottomland hardwood swamps. Riparian areas are well known to be extremely important foraging habitats for bats. For example, the majority of the activity of tricolored bats tends to occur in riparian areas, as seen in studies in Georgia (Ellis et al. 2002), South Carolina (Menzel et al. 2005*b*), and an Appalachian forest in West Virginia (Ford et al. 2005). Many species benefit from riparian areas, as bat activity of five species in South Carolina were found to be highest in riparian areas but was relatively low in upland habitats at heights around 7 and 33 feet (2 and 10 m) in intensively managed pine-dominated landscapes of the Coastal Plain (Menzel et al. 2005*b*).

Local habitat types

Bottomlands, pine forests, and upland forests are major habitat types in South Carolina used as foraging areas by bats. At the Savannah River Site, Carter et al. (2004) found that evening bats were most active in pine forests (59%) and bottomlands (37%), but rarely foraged in upland hardwoods, whereas the habitat types selected by Seminole bats included 55% pine forests, 35% bottomland hardwoods, and 11% upland hardwoods. For eastern red bats at the same site, Carter (1998) found the habitat types within their home range were 55% bottomland hardwoods, 40% pine stands, and 5% upland hardwoods. Bottomland hardwoods and pine stands were also reported as foraging areas for tricolored bats (Carter et al. 1999), and Menzel et al. (2003*b*) reported the greatest activity around lakes and ponds, bottomland hardwood forests, and grass-brush habitats. Also at the Savannah River Site, evening bats were found using gaps in bottomland hardwood and swamp forests (Menzel et al. 2001*a*). Rafinesque's big-eared bats in the mountains that had been captured and fitted with radio transmitters in the Eastatoe Valley foraged in and around forested bottomlands and a cornfield in Eastatoe Valley (Mary Bunch, SCDNR, pers. comm.). At the Silver Bluff Plantation in the Upper Coastal Plain, reproductive male Rafinesque's big-eared bats fed in uplands in young pine stands where sapling stage stands were preferred over sawtimber stands, despite the fact that mature bottomland hardwoods were common in the study area (Menzel et al. 2001*c*). Additionally in this region, southeastern bats are known to forage most actively in Carolina bay wetlands, bottomland hardwood forests, river swamps, and forest gaps (M. A. Menzel et al. 2003, Menzel et al. 2005*b*, Ford et al. 2006*a*). This species also prefers to forage over water in bald cypress-tupelo gum swamps and bottomland hardwood forests in Illinois, Arkansas, and South Carolina (Clark et al. 1998, Hoffman et al. 1998, Hoffman 1999). Pine and oak habitats are important to northern yellow bats as Krishon et al. (1997) found that the home range of a single bat was located in oak habitat the majority of the time but was also found in loblolly and slash pine communities.

Rural and urban areas play a role as foraging habitat, particularly because lights found in these areas are known to attract insects. Big brown bats forage around lights in rural areas (Geggie and Fenton 1985), and according to Menzel et al. (2001) may prefer rural rather than urban areas. Eastern red bats also feed around lights, and may land on light poles to catch moths (Barbour and Davis 1969, Hickey and Fenton 1990)

Foliage height

Bats may forage above or below tree foliage, depending in large part on their ability to navigate cluttered areas within or under the forest canopy. Brazilian free-tailed bats hunt in open spaces well above the trees of woodlands and forests, and hoary bats forage in open areas within the forest, above the forest canopy, and over lakes and streams (Shump and Shump 1982*a*, Barclay 1985, Nagorsen and Brigham 1993). Big brown bats may prefer foraging among tree foliage rather than above or below the forest canopy (Schmidly 1991), though they were more often detected above the forest canopy in a South Carolina study by Menzel et al. (2005). Tricolored bats are sometimes known to feed over the top of streamside vegetation and taller streamside trees (Caire et al. 1984, Harvey et al. 1999*a*), but along with eastern red and Seminole bats, their activity did not differ above, within, or below the forest canopy in the study by Menzel et al. (2005). Eastern small-footed bats usually forage in forest understory and canopy (Merritt 1987, Linzey 1998, Harvey et al. 1999*a*), however, migrating females foraged along streams below the canopy in New Mexico (Valdez and Cryan 2009). When studying the activity of bats at different sampling heights in five habitat types of the Coastal Plain in South Carolina, Menzel et al. (2005) found that at between 7 and 33 feet (2 and 10 m), activity was more concentrated in riparian areas compared to heights of about 98 feet (30 m) where activity was more evenly distributed across habitat types. Additionally, the levels of bat activity above the forest canopy were much greater than within or below the canopy.

Forest stand age

Foraging activity of bats is often related to forest stand age. At the Savannah River Site, Menzel et al. (2003*b*) found the most evening bat activity was highest in clearcuts and young stands, moderate in stands greater than 60 years old, and lowest in stands between 21 to 60 years old. For tricolored bats, the most activity was also in clearcuts (as well as roads and open water habitats) with moderate activity in stands four to 20 years old. However, foraging activity of big brown bats in the same study appeared to be unaffected by stand age. In the Coastal Plain of South Carolina, southeastern bats are known to forage in stands of trees between 21 to 40 years (M. A. Menzel et al. 2003, Menzel et al. 2005*b*, Ford et al. 2006*a*). Mature forests, mature deciduous uplands, and mature forested wetlands are also important roosting and foraging habitats for bats, especially northern long-eared bats (Kunz 1971, 1973, Caceres and Pybus 1997) and southeastern bats (Gardner et al. 1992, Horner 1995, Gardner 2008). Also, old growth swamp forests in South Carolina represented the majority of the area used by radio-tagged Rafinesque's big-eared bats at Francis Beidler Forest (Clark et al. 1998).

Intensively managed areas

For habitat that has been thinned or burned, bats may respond differently according to their environmental niche and habitat preferences. In relation to fire treatments in South Carolina, Loeb and Waldrop (2008) found the activity of big brown bats and eastern red bats to be significantly higher in thinned tree stands compared to control or burned stands. However, tricolored bats did not vary significantly between thinned, burned, or the control tree stands.

Forested corridors on intensively managed pine landscapes are important foraging areas for bats. For example, Hein (2008) studied six bat species in the Lower Coastal Plain and found an overall positive response to forested corridors on intensively managed pine landscapes. Compared to interior corridors or adjacent stands, there were higher occupancy rates by bats along edge habitat. Also, bat activity was negatively related to adjacent stand age and positively related to the overstory height of the corridor. At the Savannah River Site, Menzel et al. (2002*b*) studied the feeding and foraging activity of bats below the forest canopy on different timber harvest stands at three different special scales. The researchers found that on the landscape scale, more activity occurred in bottomland stands with harvested patches and around Carolina bays compared to unharvested bottomland and upland hardwoods and pines. For harvested and unharvested areas in stands where patches were harvested, activity was highest along skidder trails and forest gaps. Within individual gaps, the highest activity occurred along the forest edge. Additionally, these patterns of activity depended on the bat species.