SOUTH CAROLINA

Bat Conservation Plan

South Carolina
Department of
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SOUTH CAROLINA
BAT CONSERVATION PLAN

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This is the South Carolina Bat Conservation Plan. It provides information on legal status, public health, conservation issues, natural history, habitat requirements, species-specific accounts, threats and conservation strategies for bat species known to occur in the state. The primary purpose of this plan is to summarize available information for these species and suggest proactive strategies in order to help guide management and conservation efforts.

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Executive Summary

This is the first bat conservation plan written for South Carolina. It provides information on legal status, public health, conservation issues, natural history, habitat requirements, species-specific accounts, threats and conservation strategies for bat species known to occur in the state. The primary purpose of this plan is to summarize available information for these species and suggest proactive strategies in order to help guide management and conservation efforts.

Of the 47 bat species documented in the United States (US), 14 are found in South Carolina. These include the big brown bat (*Eptesicus fuscus*), Brazilian free-tailed bat (*Tadarida brasiliensis*), eastern red bat (*Lasiurus borealis*), eastern small-footed bat (*Myotis leibii*), evening bat (Nycticeius humeralis), hoary bat (*Lasiurus cinereus*), little brown bat (*Myotis lucifugus*), northern long-eared bat (*Myotis septentrionalis*), northern yellow bat (*Lasiurus intermedius*), Rafinesque's big-eared bat (*Corynorhinus rafinesquii*), silver-haired bat (*Lasionycteris noctivagans*), southeastern bat (*Myotis austroriparius*), Seminole bat (*Lasiurus seminolus*), and tricolored bat (*Perimyotis subflavus*). Incidental records exist of the big free-tailed bat and the federally endangered Indiana bat. However, these species are not addressed in this document due to their rarity in the state.

All of South Carolina's bat species prey on insects and are of great economic importance to the state. Insectivorous bats are known to suppress nocturnal insect populations, including crop and forest pests, and greatly reduce the need for costly pesticides. The estimated annual value of bats in pest suppression services to South Carolina's agricultural industry is nearly $115 million, with the US agricultural industry estimate at $22.9 billion (Boyles et al. 2011). The beneficial ecological effects of bats can extend past insect consumption as they indirectly suppress pest-associated fungus and the toxic compounds they produce in corn (Maine and Boyles 2015), as well as reduce the substantial impact of pesticides on many other wildlife species (Pimentel 2009).

A total of twelve, or 86% of South Carolina's bat species, are on the list of South Carolina's "Species of Greatest Conservation Need" and considered "Highest Priority" in the South Carolina State Wildlife Action Plan or SWAP (SCDNR 2015*a*). None of South Carolina's bats are listed as federally endangered, but the northern long-eared bat is listed as federally threatened. The eastern small-footed bat, Rafinesque's big-eared bat, and tricolored bat are all considered at-risk species by the USFWS. Rafinesque's big-eared bat is state endangered and the eastern small-footed bat is considered "species in need of management" or equivalent to state threatened.

All of South Carolina's bats use echolocation to identify and capture prey during flight or by gleaning insects from foliage, the surface of water, or on the ground. All of the *Myotis* species in the state, as well as the tricolored bat and Rafinesque's big-eared bat, are considered clutter-adapted species. Migratory bats are generally regarded as efficient flyers in open areas, and though many South Carolina bat species may have small seasonal movements, only the silver-haired bat is regarded as a true migrator. Other efficient open area flyers in South Carolina include the Brazilian free-tailed bat, hoary bat, northern yellow bat, eastern red bat, and

Seminole bat. Habitats used during foraging bouts by bats in the state are extremely variable and cover most habitat types available except offshore marine waters.

There are nine colonial roosting and five foliage roosting bat species in South Carolina. Of the colonial roosting species, the big brown bat, tricolored bat, and all of the *Myotis* species are known to hibernate in mines, caves, or tunnels in the state. However, half of all South Carolina bat species may use some level of torpor and wake to forage during warm winter nights. These include colonial roosting species such as the big brown bat, Brazilian free-tailed bat, and northern long-eared bat, and foliage roosting species such as the eastern red bat, northern yellow bat, Seminole bat, and silver-haired bat. Other species are known to be active year round and only enter torpor when the weather is extremely cold, such as Rafinesque's big-eared bat.

Young are generally born between May and June and most bat species in the state produce an average of two young per year, though all except one *Myotis* species gives birth to one per year. The life span of bats in South Carolina varies by species from an average of two years in the evening bat to a maximum of 30 years in the little brown bat.

One of the most devastating threats to bat populations in North America is White-nose Syndrome (WNS). Mortality rates attributed to WNS have reached up to 90 and 100% at hibernacula, causing the death of between 5.7 to 6.7 million bats since it was first documented in New York during the winter of 2006/2007. A ten-fold decrease in the numbers of bats in North American hibernacula has been attributed to WNS, and significant local extinctions in many species have resulted, including up to 69% of former hibernacula of the federally threatened northern long-eared bat in North America.

Another significant, ongoing threat is the loss and degradation of important bat roosting and foraging habitat. From the time of European settlement until around 1970, 80% of bottomland hardwood forests in the Southeast were converted for agriculture purposes. Today, urbanization has been cited as the leading threat to southern forests, and may also decrease the functional value of forests through increased fragmentation, reduced water quality, reduced carbon storage, and increased complexity in the use of fire for forest management practices. Forestry practices can also have a significant affect on bats as the felling of trees and snags, building of roads, disruption of boulders in quarries, prescribed burns, and vegetation and insect control can result in direct mortality of bats. Other major threats include human disturbance, environmental contaminants, wind energy development, and unknown impacts of various agriculture and forest management practices as well as environmental changes associated with climate change.

The conservation objectives for South Carolina's bats are to:

1. Develop Specific Action Plans
2. Continue Baseline Population Inventory and Monitoring
3. Maintain and/or Contribute to a Bat Database
4. Protect and Provide Specific Roost Sites
5. Monitor and Mitigate Emerging Threats
6. Identify, Protect, and Enhance Bat Habitat and Drinking Resources
7. Conduct Necessary Research

8. Provide Education, Extension, and Outreach
9. Partner with Agencies, Landowners, and Other Groups
10. Integrate and Maintain the South Carolina Bat Conservation Plan

Monitoring and mitigation efforts for WNS should be continued in the state to help prevent or slow the spread of the disease. Efforts that seek to protect and manage bat roosting and foraging habitat are another primary concern. Habitats of high priority have been delineated in the SWAP, and the greatest number of threatened and endangered species fall under four habitat types in the Blue Ridge ecoregion (Appalachian oak forest, high elevation forest, low elevation acidic mesic forest, and low elevation basic mesic forest) and one in the Coastal Plain (mesic forest). Other habitats utilized by over half of the state's highest priority bat species include bottomlands and riparian zones, depressions, hardwood slopes and stream bottoms, maritime forest, pine woodland, river bottoms, upland mixed forest, blackwater stream systems, rock outcrops and sandhill pine woodland.

For South Carolina's bat conservation plan to be successful, complete and reliable information on abundance, distribution, demography, life history, and habitat needs for most of South Carolina's bat species still needs to be determined. Without much of this basic ecological data, habitat protection plans and land management strategies cannot be fully informed, and therefore can only contribute limited benefits toward bat conservation. In addition, partnerships and cooperation between government agencies, private landowners, non-governmental organizations, and the general public are essential if the state is to accomplish its conservation objectives for South Carolina's bat species.

Introduction

Bats are one of the most diverse mammalian orders and compose approximately 25% of all mammals (Neuweiler 2000). With over 1,110 species in the world and 47 resident to the US, bats represent a wide range of morphological and behavioral traits. Worldwide, bats are known to consume fruit, nectar, fish, frogs, birds, mice, and the blood of livestock and wildlife. Though vampire bats tend to give other bats a bad reputation, only three vampire bat species exist in the world and none live in the US. Ecological services provided by bats in the tropics through seed dispersal and pollination are known to be vital to the survival of rainforests (Cox et al. 1991, Hodgkison et al. 2003, Kelm et al. 2008), and a popular alcoholic drink, Tequila, comes from the *Agave tequilana* plant that depends completely on bats for pollination. If that's not persuasive enough information to make one appreciate bats, consider that 70% of all bat species in the world feed exclusively on insects (Neuweiler 2000), and the amount consumed provides a substantial pest control service that would otherwise require costly pesticides. For example, in an eight county region in south-central Texas, this value was estimated at $741,000 annually for cotton producers (Cleveland et al. 2006). In the southwestern U.S. and northern Mexico, the Mexican free-tailed bat (a subspecies of the Brazilian free-tailed bat) provides a total annual cotton pest-suppression service of $11.67 million (López-Hoffman et al. 2014). The estimated annual value of bats in pest suppression services to the US agricultural industry is an estimated $22.9 billion, and is nearly $115 million in South Carolina alone (Boyles et al. 2011). The beneficial ecological effects of bats extend past insect consumption as they also indirectly suppress pest-associated fungus and the toxic compounds they produce in corn, a major worldwide crop (Maine and Boyles 2015). In addition to significant economic advantages, the presence of healthy bat populations and the reduced need for pesticides helps prevent negative effects to many other wildlife species substantially impacted by these chemicals (Pimentel 2009).

Bats have been seen as gods by the Mayans, and are highly regarded in countries like China. For example, the popular Chinese *wufu* symbol of five bats surrounding a stylized tree represents health, wealth, long life, good luck, and tranquility. Through education and outreach, as well as notoriety from WNS that has brought declining bat populations into the public spotlight, bats are beginning to be appreciated by the public and recognized for the major role they play in our ecosystem.

There is great diversity in bat populations across the state due to various roosting habits of South Carolina bats. The state itself consists of a wide variety of habitats, categorized into five distinct ecoregions: The mountainous Blue Ridge near the Appalachians, the Piedmont composed of foothills and midlands, the Sandhills composed of sandy soils and rolling hills along the Fall Line, the Coastal Plain composed of swamps and marshes with rolling hills in the innermost portion and flat plains in the outermost portion, and the Coastal Zone, a warmer, seaward extension of the Coastal Plain composed of sand flats, pine hardwood, swamps, and emergent saltwater marshes (Figure 1). South Carolina commonly harbors 14 bat species, the diversity of which vary geographically across the state (Table 1). Eight bat species occur statewide, and these are also the only bats present in the Piedmont. Incidental records exist of the big free-tailed bat (*Nyctinomops macrotis*) and the federally endangered Indiana bat (*Myotis sodalis*): however, these species are not addressed in this document due to their rarity in the state.

Of the bat species occurring in South Carolina, five are considered foliage roosting bats and nine are considered colonial roosting bats. As the names suggest, colonial roosting bats roost in colonies in winter hibernacula in caves and mines, and foliage roosting bats typically roost solitarily in the foliage of trees. The foliage roosting bats of South Carolina include all of the species in the *Lasiurus* genus and *Lasionycteris* genus and are the eastern red bat, hoary bat, northern yellow bat, Seminole bat, and silver-haired bat. The colonial roosting species include all the species in the *Myotis* genus and the rest of the bats in the state. These are the eastern small-footed bat, little brown bat, northern long-eared bat, southeastern bat, big brown bat, Brazilian free-tailed bat, evening bat, Rafinesque's bat, and tricolored bat.

Like many bat species across the US, the population status and ecology of most bats in South Carolina remain unknown (Menzel et al. 2003*b*). We seek to summarize available information on legal status, public health, conservation issues, natural history, habitat requirements, species-specific accounts, threats and conservation strategies in 4 chapters: 1. Status and Conservation Issues, 2. Natural History and Habitat Requirements, 3. Species Accounts, and 4. Conservation Actions and Strategies. Chapter 1 is an overview of the legal and conservation status of bats in the state, relationships to public health, and conservation threats and management activities. Chapter 2 summarizes the natural history and habitat requirement of South Carolina's bats. Chapter 3 provides informational accounts of all 14 species on identification, status, life history traits, and specific conservation threats and measures. Chapter 4 is a strategic outline of conservation tasks that could help protect South Carolina's bat populations.

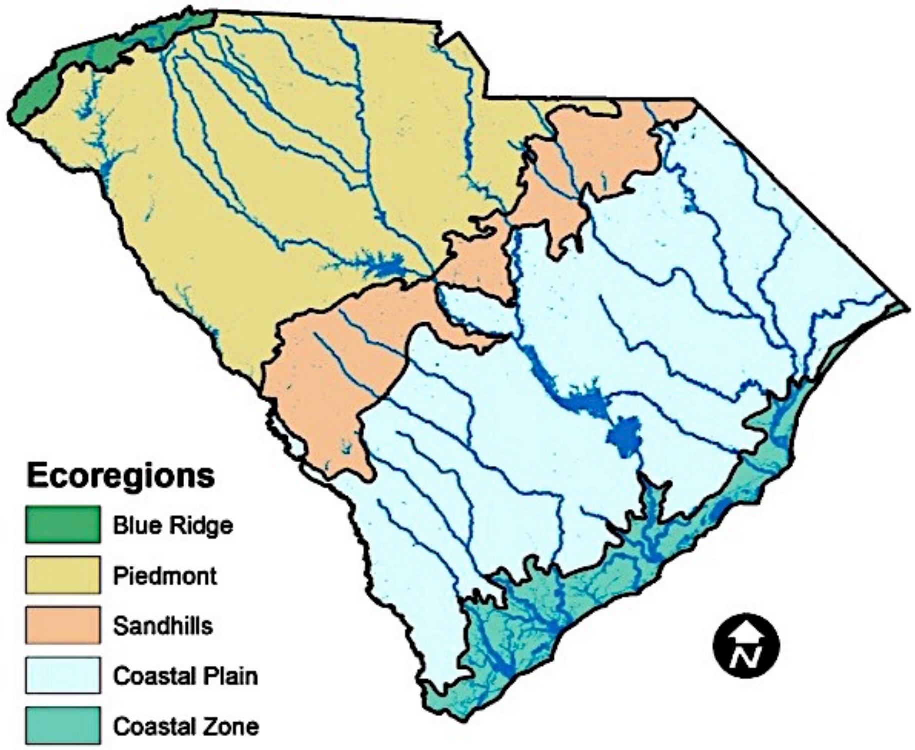

Figure 1: The five ecoregions of South Carolina. Modified from Griffith et al. (2002) for the South Carolina State Wildlife Action Plan (SCDNR 2015*a*). The Coastal Plain-Coastal Zone boundary is modified to conform to the legal delineation of the boundary between freshwater and saltwater zones for fisheries management purposes.

Table 1: Bat species and their associated ecoregions documented in South Carolina. Presence in parentheses (X) indicates that the species is not often found in that ecoregion.

		Ecoregion				
Common Name	**Scientific Name**	**Blue Ridge**	**Piedmont**	**Sandhills**	**Coastal Plain**	**Coastal Zone**
Big Brown Bat	*Eptesicus fuscus*	(X)	X	X	X	X
Brazilian Free-tailed Bat	*Tadarida brasiliensis*	X	X	X	X	X
Eastern Red Bat	*Lasiurus borealis*	X	X	X	X	X
Eastern Small-footed Bat	*Myotis leibii*	X				
Evening Bat	*Nycticeius humeralis*	X	X	X	X	X
Hoary Bat	*Lasiurus cinereus*	X	X	X	X	X
Little Brown Bat	*Myotis lucifugus*	X		(X)	(X)	(X)
Northern Long-eared Bat	*Myotis septentrionalis*	X				
Northern Yellow Bat	*Lasiurus intermedius*			X	X	X
Rafinesque's Big-eared Bat	*Corynorhinus rafinesquii*	X		X	X	X
Seminole Bat	*Lasiurus seminolus*	(X)	X	X	X	X
Silver-haired Bat	*Lasionycteris noctivagans*	X	X	X	X	X
Southeastern Bat	*Myotis austroriparius*			X	X	X
Tricolored Bat	*Perimyotis subflavus*	X	X	X	X	X
		12	*8*	*12*	*12*	*12*

Chapter 1: Status and Conservation Issues

Legal and Conservation Status

All South Carolina bat species are protected on public lands, including those managed and/or owned by both State and Federal resource agencies such as state wildlife management areas, heritage preserves, and national forests. Additional protection may be provided on lands owned or operated by non-profit conservation organizations such as The Nature Conservancy, National Audubon Society, and local and national Land Trust Organizations.

Federal

Of the 14 bat species in South Carolina, none are federally listed as endangered, one is federally listed as threatened with an interim 4(d) rule (northern long-eared bat), two are being evaluated by the USFWS to determine if listing under the ESA is warranted (little brown bat and tricolored bat), and three are considered at-risk species by the agency (eastern small-footed bat, Rafinesque's big-eared bat, and tricolored bat) (Table 2).

In June of 2011, a status review of the eastern small-footed bat and the northern long-eared bat was initiated. In October 2013, the USFWS announced a 12-month finding on a petition to list the eastern small-footed bat and the northern long-eared bat as endangered or threatened under the ESA and found that the eastern small-footed bat did not warrant listing (USFWS 2013) but proposed a status of Endangered for the northern long-eared bat due to threats from WNS. In April 2015 it was determined the northern long-eared bat met the ESA definition of Threatened, and 30 days later the listing became effective with an interim 4(d) rule providing flexibility to specific entities who conduct activities in northern long-eared bat habitat (USFWS 2015*a*). Currently, a USFWS petition is being addressed for the little brown bat (Kunz and Reichard 2010), and a status review is being conducted for the tricolored bat.

Federally threatened northern long-eared bat and 4(d) rule exemptions

The following information from the USFWS (2015) applies to projects that could result in take (defined by the ESA as "to harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect, or to attempt to engage in any such conduct") of northern long-eared bats within the range of the northern long-eared bat and the WNS Buffer Zone (see map at http://www.fws.gov/midwest/nleb/WNSBuffer.pdf). South Carolina counties within these areas include Abbeville, Anderson, Cherokee, Greenville, Laurens, Oconee, Pickens, Spartanburg, Union, and York. Though the section below attempts to explain the interim 4 (d) rule, federal agencies that carry out, fund, or authorize projects that may affect northern long-eared bats are required to have a formal USFWS consultation. A formal consultation is not required only if a federal action agency determines that no effect to northern long-eared bats is expected. For more information, please contact Morgan K. Wolf at (843) 727-4707 ext. 219, or morgan_wolf@fws.gov at the USFWS Charleston office.

Section 9 of the Endangered Species Act prohibits take of a wildlife species listed under the ESA as threatened unless specifically authorized by regulation. Any purposeful take of northern long-eared bats for removal from a human structure, or by individuals authorized to conduct capture or related activities for other bats listed under the

Table 2: Federal and state conservation status of bat species in South Carolina.

		Federal	State		
Common Name	**Scientific Name**	**USFWS[a]**	**SCDNR[b]**	**SCDNR Heritage Trust[c]**	
Big Brown Bat	*Eptesicus fuscus*		SGCN	G5	S5
Brazilian Free-tailed Bat	*Tadarida brasiliensis*			G5	SNR
Eastern Red Bat	*Lasiurus borealis*		SGCN	G5	SNR
Eastern Small-footed Bat	*Myotis leibii*	ARS	ST, SGCN	G1G3	S1
Evening Bat	*Nycticeius humeralis*			G5	SNR
Hoary Bat	*Lasiurus cinereus*		SGCN	G5	SNR
Little Brown Bat	*Myotis lucifugus*		SGCN	G3	S3?
Northern Long-eared Bat	*Myotis septentrionalis*	T	ST, SGCN	G1G2	S4*
Northern Yellow Bat	*Lasiurus intermedius*		SGCN	G4G5	SNR
Rafinesque's Big-eared Bat	*Corynorhinus rafinesquii*	ARS	SE, SGCN	G3G4	S2?
Seminole Bat	*Lasiurus seminolus*		SGCN	G5	SNR
Silver-haired Bat	*Lasionycteris noctivagans*		SGCN	G5	SNR
Southeastern Bat	*Myotis austroriparius*		SGCN	G3G4	S1
Tricolored Bat	*Perimyotis subflavus*	ARS*	SGCN	G3	SNR

[a]U.S. Fish and Wildlife Service: T = Federally Threatened, ARS = At-Risk Species that the FWS has been petitioned to list and for which a positive 90-day finding has been issued (listing may be warranted); information is provided only for conservation actions as no Federal protections currently exist, ARS* = At-Risk Species that are either former Candidate Species or are emerging conservation priority species.

[b]South Carolina Department of Natural Resources: SE = State Endangered, ST = State Threatened, SGCN = Species of Greatest Conservation Need and highest priority

[c]NatureServe: G = global, S = state, 1 = critically imperiled, 2 = imperiled, 3 = vulnerable to extirpation or extinction, 4 =apparently secure, 5 = demonstrably widespread, abundant, and secure, * = rank will be lowered in the near future. Rankings taken from Master et al. 2012.

Endangered Species Act within one year of the effective date of the interim 4(d) rule, are exempted by the 4(d) rule. To clarify, this means that no permit or consultation is required to exclude northern long-eared bats from a home. Researchers and biologists conducting actions relating to capture, handling, attachment of radio transmitters, and tracking of northern long-eared bats will be required to obtain a federal scientific collection/recovery permit under Section 10(a)(1)(A) of the ESA.

Incidental take of northern long-eared bats is allowed for actions outside of the WNS Buffer Zone (see map above). Incidental take within the WNS buffer zone not related to specific forest management, native prairie management, minimal and hazardous tree removal, and maintenance or expansion of existing rights-of-way and transmission corridors, as outlined in the 4(d) rule, are not exempted by the 4(d) rule and may require an incidental take permit under Section 10(a)(1)(B) of the ESA. Forest management that converts mature hardwood, or mixed, forest into intensively managed monoculture pine plantation stands, or non-forested landscape, is not exempted under the 4(d) interim rule since these plantations provide poor-quality bat habitat. Minimal tree removal only refers to an impact of one acre or less of contiguous habitat or one acre total within a larger tract. If a northern long-eared bat maternity roost tree or hibernacula has been documented on or near the project area for forest management, native prairie management, minimal and hazardous tree removal, and maintenance or expansion of existing rights-of-way and transmission corridors projects, incidental take will be exempted by the 4(d) rule if activities are not conducted within ¼ mile of known, occupied hibernacula; a known, occupied roost tree from June 1 to July 31 (during the pup season) is not cut or destroyed; and clearcuts are not conducted within a ¼ mile of known, occupied roost trees from June 1 to July 31. Otherwise, an incidental take permit under Section 10(a)(1)(B) of the ESA may be necessary for these activities.

Caves on federal land

Significant caves on federal lands are secured, protected, and preserved by federal land managers through the Federal Cave Resources Protection Act of 1988 (18 U.S.C. § 4301–4309). Caves on federal land generally fulfill the "significant" cave definition, meaning those with characteristics pertaining to biological, geological, mineralogical, paleontological, hydrological, cultural, recreational, educational, or scientific resources. Specific locations of caves and mines are not disclosed for their protection (16 U.S.C § 4304(a)). Additionally, in 2011 the US Forest Service (USFS) authorized closure to human entry of all caves and abandoned underground mines in the Southern Region for five years in order to protect caves, mines, and/or associated wildlife species from the spread of *Pseudogymnoascus destructans*, the fungal agent causing WNS, through human transmission (USFS 2011).

State

One bat species in South Carolina is state endangered (Rafinesque's big-eared bat), and one is a "species in need of management" or equivalent to state threatened (eastern small-footed bat). A total of twelve, or 86% of South Carolina's bat species, are on the list of South Carolina's "Species of Greatest Conservation Need" and considered "Highest Priority" in the South Carolina State Wildlife Action Plan (SCDNR 2015*a*) (Table 2). This high proportion is not limited to South Carolina as 15 years ago, before WNS was even detected, 87% of bat species in the Southeast had special conservation designations (Laerm et al. 2000).

State endangered and state threatened bat species are protected under the South Carolina Nongame and Endangered Species Conservation Act (§50-15-10 et seq.). For State endangered species (CL 50-15-30(C), Appendix A), violation of the law is a misdemeanor and a fine of $1,000 or imprisonment up to a year, or both (CL 50-15-80(B), Appendix A). There is less stringent protection for species recognized as state threatened or species "in need of management" (CL 50-15-20(C), Appendix A). This designation roughly parallels the federal threatened species statute and establishes South Carolina Department of Natural Resources (SCDNR) as the authority to engage in conservation activities and develop management programs so these species can "sustain themselves successfully." Violation of this law is a misdemeanor, a fine of up to $500 or imprisonment up to 30 days, and restitution paid (CL 50-15-80(A), Appendix A).

The collection of any bat species in South Carolina for scientific or propagating purposes requires a scientific permit (CR 123-150.3, Appendix A). Violation of the law is a misdemeanor and a fine of between $25 and $100, imprisonment up to 30 days, and revocation of the permit (CL 50-11-1180, Appendix A).

Any bat species may be removed from a home in South Carolina without a permit or consultation. If it is necessary to protect human health and there is no immediate threat to human life, a permit may be issued to remove, capture, or destroy an endangered species. In the case of an immediate threat to human life, no permit is required to remove, capture, or destroy threatened or endangered or species in need of management (CL 50-15-40(E), Appendix A). Additionally, the department may permit taking, possession, transportation, exportation, or shipment of species which appear on the state list of endangered species, or federal list of threatened or endangered species, for scientific, zoological, or educational purposes, for propagation in captivity of such wildlife, or for other special purposes (CL 50-15-40(D), Appendix A).

All South Carolina bats are protected on Heritage Preserves and SCDNR owned lands (CL 50-11-2200 (C), Appendix A). Violation of the law is a misdemeanor, and may require restitution to the land owner, a fine of between $200 and $500 or imprisoned for up to 30 days or both, loss of privilege to enter these lands for two years, and loss of privilege to hunt and fish for one year (CL 50-11-2210, CL 50-11-2220, Appendix A).

The Heritage Trust Program of the SCDNR protects critical natural habitats and significant cultural sites in the form of heritage preserves. This program identifies conservation ranks for South Carolina bat species according to NatureServe criteria, which can be seen in Table 2.

Public Health

Rabies

Rabies is a viral disease transmitted through mammals that infects the central nervous system and is fatal to humans if not treated early. The vast majority of cases reported annually occur in raccoons, skunks, foxes, and insectivorous bats (Center for Disease Control 2015). Transmission usually occurs when infected saliva of a host is passed through bites and scratches, though there have been very rare cases of infected saliva coming into contact with mucous membranes (i.e., eyes, nose, mouth) (Brass 1994). If a suspected or confirmed rabies exposure occurs, development of rabies can be prevented by immediately contacting a doctor and the local health department, and the individual will be treated with a series of intramuscular injections of postexposure prophylaxis of human antirabies immunoglobulin over a 14-day period. For people who handle bats or come into regular contact with wild and feral mammals, such as veterinarians, animal control officers, wildlife biologists and rehabilitators, a preexposure prophylaxis is recommended (Krebs et al. 1995).

In the U.S. annually, the average number of people that die from rabies is one to two, and the animal that caused the infection is not known in the majority of cases. Deaths from rabies in the U.S. often happen because individuals aren't aware of their exposure and don't seek prompt post-exposure treatment. Particularly in developing countries, humans are typically exposed to rabies through unvaccinated dogs and cats. In the U.S., vaccination of dogs has led to a major decline of rabies cases in humans since the 1940s (Brass 1994), and today rabies is limited mostly to contact with wild animals. Exposure to infected bats accounts for many of these wild animal cases since the 1980s (Childs et al. 1994, Hoff et al. 1993, Krebs et al. 1995), and in recent years the proportion of rabies cases from bat bites has increased (Rupprecht et al. 2001). Rabies strains in bats differ from those in terrestrial mammals, meaning it's possible to determine routes of human exposure by animal type. Most human deaths from rabies have been found to be from unrecognized exposure to animals infected with bat-variant rabies (Messenger et al. 2003). In the U.S. from 1980 to 1994, 11 of the 14 confirmed cases of human rabies were linked to bats, eight of which were associated with the rabies virus variant in silver-haired bats (Krebs et al. 1995). Big brown bats, little brown bats, and tricolored bats are species found in South Carolina that could potentially carry this silver-haired bat rabies viral strain (Messenger et al. 1997). Rabies has also been documented in most other bat species occurring in the state, including hoary bat, eastern red bat, northern yellow bat, Seminole bat, eastern small-footed bat, southeastern bat, evening bat, silver-haired bat, Brazilian free-tailed bat, and Rafinesque's big-eared bat (Constantine 1979*a*, Menzel et al. 2003*a*, Sasse and Saugey 2008). The Centers for Disease Control and Prevention statistics have indicated that only about 10% of all annually reported and confirmed rabid animals are from bats (Krebs et al. 1995). This statistic holds true for South Carolina, as of the 613 animals that tested positive for rabies in the state from 2010 to 2014, 51% were raccoons, 17% skunks, 15% foxes, 8% bats, 5% cats, 2% dogs, and 1% other wild animals (SCDHEC 2014). In a study looking at the distribution of bats species submitted for rabies testing between 1970 and 1990 in South Carolina, 231 out of 2,657 bats submitted were found to be rabid. The eastern red bat was submitted most frequently for testing (30%), and had the highest prevalence of rabies (18%) (Parker et al. 1999). However, bats turned in to be tested compared to those randomly sampled from the environment show very different rates of rabies prevalence, and depends on bat species, colony, and location (Brass 1994, Klug et al. 2011). Klug et al. (2011) studied bat species with the highest reported prevalence of rabies in North America, the hoary bat and the silver-haired bat, and compared bats turned in by the general public to random samples. They discovered that overall rabies prevalence is actually less than or equal to 1%. Though fears and misconceptions about health risks from rabies have resulted in unnecessary eradication (Pierson 1998), the overall human health risks posed by rabid bats in North America is very low and unprovoked attacks by rabid bats on humans is incredibly rare (Constantine 1979*b*, Krebs et al. 1995, Rotz et al. 1998, Tuttle and Kern 1981).

Most routes of contact and potential rabies transmission can be avoided by simple preventive measures. The majority of contact between humans and sick bats occurs when cats bring bats home to their owners (Constantine 2009), and species such as big brown bats that occur in or near buildings may pose a greater risk of rabies transmission to humans (Childs et al. 1994). Preventative measures that reduce the risk of rabies exposure include ensuring dogs and cats are vaccinated against rabies, avoiding handing wildlife, avoiding entry into caves, attics, or abandoned buildings that contain bats, preventing bats from roosting in buildings, and evicting bats through exclusion methods instead of chemical poisons. For a useful guide to bat exclusion, see Bats in Buildings: A Guide to Safe & Humane Exclusions by Bat Conservation International (https://www.batcon.org/pdfs/education/fof_ug.pdf).

Histoplasmosis

Histoplasmosis is a potentially fatal disease affecting the lungs caused by *Histoplasma capsulatum*, a fungus known to thrive in moderate temperatures and moist environments. Spores of this fungus are found in soil with bat or bird droppings, and when the soil is disturbed the spores may be readily released into the air, causing infection through inhalation of the contaminated soil. Symptoms are similar to those associated with the flu and include fever, chills, headache, muscle aches, dry cough, and chest discomfort. The disease can be fatal to infants and individuals with compromised immune systems such as older adults, or to those who may receive high doses such as farmers, cave explorers, or guano miners (American Lung Association 2015, Emmons 1949, De Monbreun 1934).

Histoplasmosis is endemic to South Carolina, and in 1979 an outbreak of 10 cases of histoplasmosis occurred following the clearing of a blackbird roosting area (DiSalvo and Johnson 1979). However, the disease is most commonly found in areas surrounding the Ohio and Mississippi River valleys and rates are highest in the Midwest, especially among older adults (Baddley et al. 2011). Preventative measures include avoiding exposure, spraying contaminated soil, and/or using a well-fitting respirator capable of filtering particles with a diameter of two microns (Constantine 1993). Persons working in bat guano should consult the Center for Disease Control website at http://www.cdc.gov/fungal/diseases/histoplasmosis/.

Conservation Issues

White-nose Syndrome

White-nose Syndrome (WNS) is a disease caused by a white fungus species *Pseudogymnoascus* (formally *Geomyces*) *destructans (P.d.)* that forms on the nose, wing membranes, and ears of affected hibernating bats. A bat may be infected with WNS and not show signs of fungal growth, so histopathology may be required to confirm the disease (Meteyer et al. 2009). This fungus erodes the outer epidermis and infects underlying skin and connective tissue, causing inflammation. Hypotheses from the ultimate cause of mortality from WNS include the inability to function normally due to skin and wing damage (Cryan et al. 2010), shorter torpor bouts leading to the premature burning of fat reserves and causing starvation (Reeder et al. 2012), or increased evaporative water loss and dehydration (Willis et al. 2011) which could also lead to starvation from frequent waking due to thirst. However, a recent paper by Verant et al. (2014) suggests that fat reserves are prematurely burned before wing lesions or aberrant behavior such as shorter torpor bouts occur.

The devastating effect of WNS on North American bat populations have been unprecedented. Mortality rates attributed to WNS have reached up to 90 and 100% at hibernacula (Kunz and Tuttle 2009) causing the death of between 5.7 to 6.7 million bats in North America since it was first documented in New York during the winter of 2006/2007 (USFWS 2012). At the end of the 2014/2015 winter season, WNS had been confirmed in bats in 26 states and five Canadian provinces, and *P.d.* confirmed in three additional states (Figure 2) (USFWS 2015*b*). A ten-fold decrease in the numbers of bats in North American hibernacula has been attributed to WNS, and significant local extinctions in many species have resulted, including up to 69% of former hibernacula of the now federally threatened northern long-eared bat (Frick et al. 2015).

Among bat species currently confirmed to be affected by WNS in other states, five occur in South Carolina. These species are all colonial cavity roosting bats, mainly from the *Myotis* genus. They include the big brown bat, eastern small-footed bat, little brown bat, northern long-eared bat, and tricolored bat. Two of these species have been confirmed with the disease in South Carolina so far. WNS was first confirmed in South Carolina

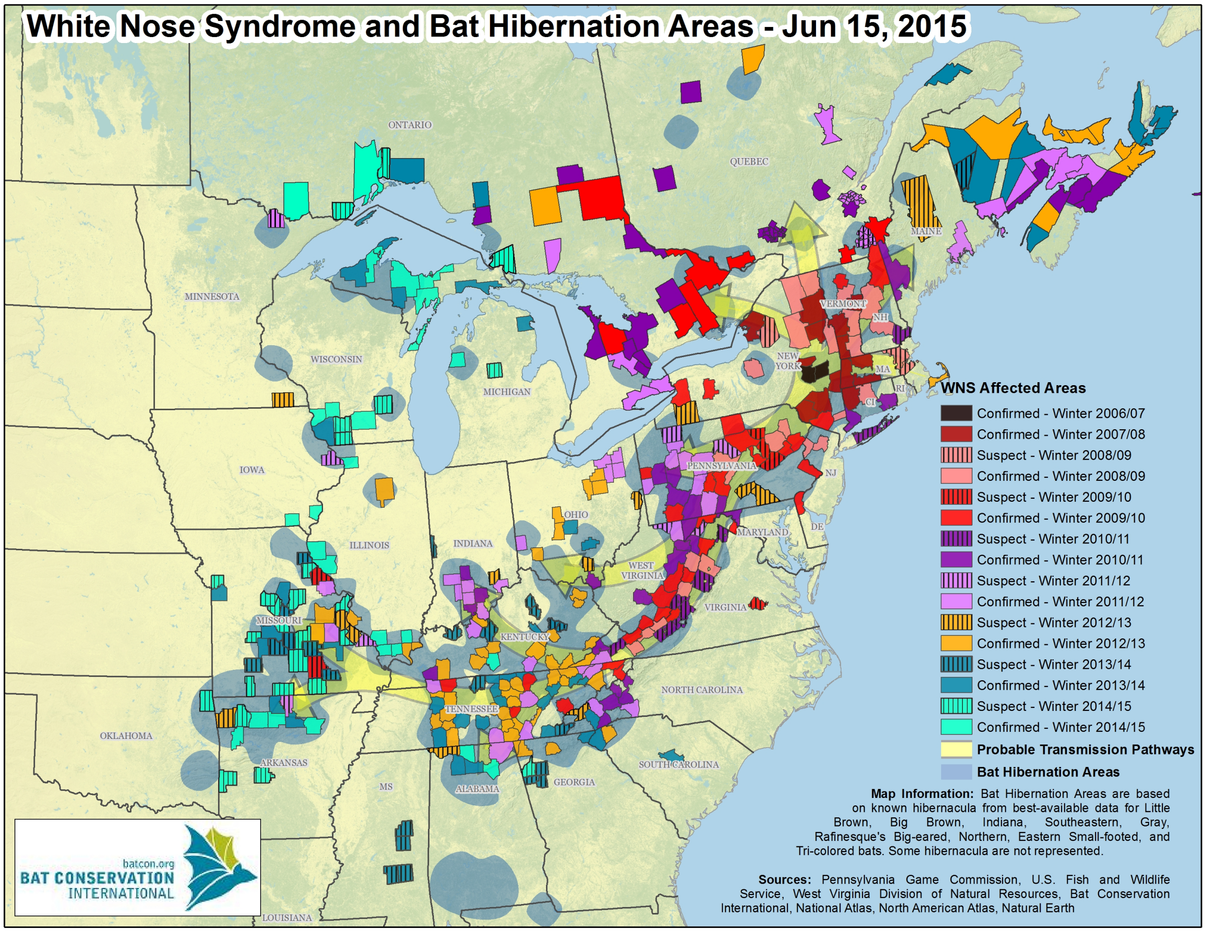

Figure 2: The occurrence and spread of WNS in North America

in Pickens County on a tricolored bat (*Perimyotis subflavus*) in March of 2013. Since then, another case in Pickens county on an eastern small-footed bat (*Myotis lebii*) and two other cases in Oconee and Richland counties on tricolored bats have been reported in 2013 and 2014. Oconee county was also found to have *P. d.* in an old mine in 2015, making it an additional suspected WNS affected area. Also during 2015, dead tricolored bats were found at the main Stumphouse Tunnel, one of which was tested and confirmed to have WNS.

P. d. has been detected on additional bat species in other states, but have not yet shown diagnostic signs of the disease. These species include two colonial cavity bat species, the southeastern bat and Rafinesque's big-eared bat, and two species that generally roost in foliage, the eastern red bat and silver-haired bat. The fungus was found on these bats while roosting in caves.

Significant over-winter mortality caused by WNS has been seen in little brown bat, northern long-eared bat and tricolored bat populations (Turner et al. 2011). WNS killed at least one million little brown bats from 2006 to 2010 and caused severe declines in abundance in the eastern portion of its range (Frick et al. 2010*a*, Kunz and Reichard 2010). The core region where much of the global population of little brown bats occur is now infected with WNS, and threatens to push these populations to extinction by 2026 (Frick et al. 2010*a*, Kunz and Reichard 2010). Across large portions of the eastern small-footed bats' range in New York, Massachusetts, and Vermont, populations declined 78% overall between 2006 and 2009 due to this disease (Langwig et al. 2009). Eastern small-footed bats are also at a greater risk of infection by WNS due to their tendency to roost near the entrance of hibernacula where exposure may be increased. Northern long-eared bats are particularly vulnerable to WNS threats due to life history traits that make them slow to recover, such as low fecundity (Caceres and Barclay 2000, Caceres and Pybus 1997). According to Alves et al. (2014), an expected relative population reduction for eastern small-footed bats and northern long-eared bats is estimated to be 71.2% and 31.3% in intermediate population-reduction scenarios, 96.6% and 42.4% in pessimistic scenarios, and 29.3% and 12.9% in optimistic scenarios, respectively. Interestingly, the big brown bat seems highly resistant to WNS, limiting the degree of infection by *P. d.* to the outer epidermis during torpor (Frank et al. 2014).

The common thread between species affected by WNS is that they're colonial cavity roosting bats that hibernate in cold, humid environments. This predisposes them to infection by *P. d.* because the fungus survives in darkness in very similar temperatures from 36 to 57°F (2 to 14°C), (though it thrives in 55 to 60°F, or 12.5 to 15.8°C) and humidity of >90%; and the fact that bats suppress their immune system while in torpor during hibernation (Blehert et al. 2009, Lorch et al. 2013, Verant et al. 2012). Also, the rapid spread of the fungus across eastern North America is likely due to the fact that many of these bats hibernate in clusters and healthy bats can readily come in contact with infected bats (Langwig et al. 2012). Additionally, the spores of *P. d.* persist in caves year round and may be spread by humans on gear and clothing (Okoniewski et al. 2010), as well as by other bats and animals.

While there is promising research showing that bacteria native to North American soils (Cornelison et al. 2014) and bacteria from the skin of bats (Hoyt et al. 2015) can inhibit the growth of *P. d.*, there are currently no treatments available to reduce the spread of WNS.

Habitat Loss and Alteration

Urbanization

South Carolina has one of the fastest growing populations in the U.S. (Strom Thurmond Institute 1998). Growing from less than 2.5 million in 1960 to over four million in 2000, it's expected to reach over five million by 2030 (SCFC 2010). Much of this growth results in the conversion of forestland to residential areas in the form of urban sprawl (Macie and Hermansen 2002, Slade 2008).

Urbanization has been cited as the leading threat to southern forests, and Wear and Greis (2011) anticipate a minimum 7% forest loss over the next 50 years. In addition to this is the decrease in the functional value of forests through increased fragmentation, reduced water quality, reduced carbon storage, and increased complexity in the use of fire for forest management practices. According to the South Carolina Forestry Commission (2010), much of urbanized land being converted from highly productive forest land no longer provides water quality protection, and is now uninhabitable to most wildlife species. For example, expanding urbanization is one of the major factors contributing to the loss of bottomland hardwood forest critical to bat species in the southeast (Loeb et al. 2011, Smith et al. 2009). Also, residential development and citrus grove plantations may threaten northern yellow bats if they result in the loss of sandhill and oak hammock habitats

(Humphrey 1992). Lastly, the threat of wildfires increases with the increasing human population (SCFC 2010), and blue jays (*Cyanocitta cristata*) in suburban areas may be a potential threat to species such as hoary bats (Bolster 2005).

Though there are programs seeking to mitigate these negative effects and promote healthy urban forests, such as the South Carolina Forestry Commission's Urban & Community Forestry Program, productive forest land habitat needed by bats is often lost through urbanization. In addition, many forms of habitat alteration may inadvertently increase predation by natural predators and unnatural predators such as feral cats.

Agricultural Land Use

Historically, the primary cause of deforestation in South Carolina was due to the conversion of land for agricultural purposes. In the Southeast, 80% of bottomland hardwood forests were converted for agriculture purposes from the time of European settlement until around 1970 (Wear and Greis 2002). However, between 1968 and 2006, South Carolina's agricultural land decreased by 60% or two million acres (SCFC 2010). Today, South Carolina has approximately 4.9 million acres of farmland, or 25.8% of the state's land area (London 2015). The market value (total cash receipts) of agricultural products sold in 2012 totaled over $2.9 billion and the top five agricultural commodities were: 1) poultry (broilers), 2) turkeys, 3) greenhouse/nursery, 4) cotton, and 5) corn (United States Department of Agriculture Economic Research Service 2015).

Conversion of land to agricultural production has been one of the major factors contributing to the loss of bottomland hardwood forest (Loeb et al. 2011, Smith et al. 2009). However, since agricultural lands are now being converted into either urban uses or forest land, loss of habitat from the conversion of forest for agricultural purposes is not a primary concern compared to other threats. Instead however, agrochemicals may negatively impact bat prey availability in existing agricultural areas. A study by Wickramasinghe et al. (2004) found there was a significant increase in insect abundance, species richness, and moth species diversity on organic farms that used no agrochemicals compared to conventional farms, and that five insect families were significantly more abundant on organic farms. No research has been conducted to assess the impacts of agriculture on bats in South Carolina, but in 2011, only 802 acres of the 4.9 million acres of farmland in the state were organic (United States Department of Agriculture Economic Research Service 2015).

Hydrological Alteration

In the past, habitats such as bottomland hardwood forests relied on natural cyclic-flooding events to thrive. Natural riparian areas provided high water quality and benthic habitat in the form of coarse woody debris for insect larvae, prevented sedimentation collection, and provided cooler temperatures from the shade of trees (Anbumozhi et al. 2005, Broadmeadow and Nisbet 2004, Gilliam 1994). Carolina bays also provided various wetland functions such as nutrient cycling and biodiversity conservation (Bennett and Nelson 1991, Sharitz and Gresham 1998).

Disturbance patterns occurring naturally are complicated and influenced by a multitude of variables (King and Antrobus 2001), and the affects of human-made hydrological alterations on these natural processes can have unfavorable and unplanned results on bat habitat through change in forest composition and structure. For example, extensive flooding caused or exacerbated by anthropological land use changes can lead to significant stress on forest productivity (Megonigal et al. 1997) or direct mortality such as in the death of 57,000 bats in Florida (Gore and Hovis 1994). In addition, ditches, channels and impoundments can change water temperature as well as facilitate high sediment loads into wetlands, which affects ecosystem richness and productivity by covering aquatic vegetation, increasing turbidity, and reducing oxygen content. Impoundments also decrease water circulation, preventing outflow of nutrients, changing dissolved oxygen and pH levels, and increasing the accumulation of toxic substances in sediments (US Environmental Protection Agency 1993).

Altered hydrology can also cause habitat fragmentation, which is associated with numerous negative impacts to wildlife (Fleming et al. 1994, Harris 1988). Approximately 97% of Carolina bays have been disturbed in South Carolina (Bennett and Nelson 1991, Sharitz and Gresham 1998), and fragmented bottomland hardwood forests may have a reduced capacity to store flood water, trap nutrients, recharge groundwater, and provide wildlife habitat (Mississippi Museum of Natural Science 2005). Alteration of natural flood regimes may also affect the regeneration of important forest community types such as cypress-gum, thus preventing recruitment of future roost trees (Bunch et al. 2015*b*). Altered hydrological regimes could also cause the outright loss of cypress and tupelo gum swamps, bottomland hardwood, and other forested wetlands, and the loss of these habitats are known to contribute to the decline of bat species (Mirowsky and Horner 1997).

Forest Management

Forestry is the leading manufacturing industry in South Carolina when it comes to employment and labor income, and timber is the number one harvested crop. South Carolina has approximately 13.1 million acres of forest, occupying 68% of the state's land area. Of South Carolina's forests, 53% (6.9 million acres) are characterized as hardwood forest and 47% (6.2 million acres) as softwood (SCFC 2014).

The majority (88%) of South Carolina's forest is privately owned, with individual ownership at 58%, corporate ownership at 24%, and forest industry at 6% (Figure 3). Only 12% is owned by public agencies, and includes national forests at 5%, state, county and municipal lands at 4%, and other federal land at 3% (Conner 2011, SCFC 2010).

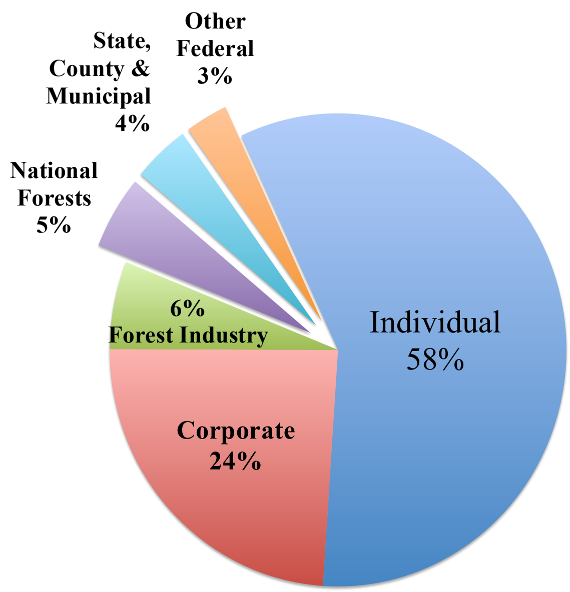

Figure 3: Forest land ownership in South Carolina (Conner 2011, SCFC 2010).

Forest industry has declined markedly in the past decade, and between 2001 and 2012 it was reduced by 88%. This decline continues today as forest land is transferred to private individuals and non-forest industry corporations. Because 11 million of the 13 million acres of forest are privately owned, this land is at risk for development. About one-fifth of these private individuals considered timber products from their land an important management objective, but there is concern that these forests will become increasingly parceled into smaller holdings, fragmented, and/or converted to non-forest uses (SCFC 2010).

Forests in the South have been fragmented and reduced in functionality and extent from various causes including timber harvesting practices (Noss et al. 1995, Wear and Greis 2002). Forest management has direct and indirect impacts on bats since these species have a close association with forest structure and vegetation (Guldin and Emmingham 2007). The felling of trees and snags, building of roads, disruption of boulders in quarries, prescribed burns, and vegetation and insect control are all forestry practices that can result in direct mortality of bats (Hayes and Loeb 2007). Indirect impacts from forest management have the potential to be greater and make lasting affects on bat populations due to their cascading nature. For example, the removal of mature, large-diameter trees and snags through commercial timber operations in the southeastern US (Gooding and Langford 2004, Wilson et al. 2007) reduces important roost availability for many bat species since tree size and stand age are important indicators of cavity abundance (Allen and Corn 1990, Barclay and Kurta 2007, Fan et al. 2003). The loss of existing snags and curtailed development of large snags from forestry practices means less maternity and roosting sites for silver-haired bats (Betts 1998, Campbell et al. 1996, Mattson et al. 1996). Additionally, loss and degradation of bottomland hardwood forest habitat through clearing and drainage along with the disappearance of extra large tree hollows has likely been a contributing factor in the vulnerability of Rafinesque's big-eared bats (Clark 2000, Mitsch and Gosselink 2001, Tiner 1984). Even if roosts aren't directly affected, forest fragmentation around roosts may increase the distance bats have to fly in order to find suitable foraging and drinking areas, and can lead to long-term declines in bat colony sizes (Adams and Hayes 2008, Clark 1990, Hurst and Lacki 1999). Forest management activities such as thinning effect the amount of vegetative clutter and tree density in a forest, which are factors strongly related to bat activity and can actually have a positive impact on certain species (Hayes and Loeb 2007). Additionally, because riparian zones are important to bats, providing a riparian zone buffer during timber harvests would help minimize the impact to bats. The functional width of riparian buffer zones near small streams, according to a study by O'Keefe et al. (2013), is greater than or equal to 32 feet (10 m). However, research on larger buffer zone sizes still needs to be conducted.

Currently, South Carolina has more forest land and timber volume than ever recorded. However, due to the creation of large portions of young forest in a short period of time through the Conservation Reserve Program and Hurricane Hugo reforestation efforts, much of these tree stands are of similar age (SCFC 2010). This lack of age and size class diversity does not provide as wide an array of habitat for bats as a similar area with more diversity might. Studies show that monotypic stands don't provide quality foraging areas for bats, as the abundance of moth prey is reduced and foraging success is lowered (Lacki and Dodd 2011, Summerville and Crist 2002). For example, even-age timber management practices could have an adverse affect on the threatened northern long-eared bat because mature forest stands are important habitat to this species (Caceres and Pybus 1997). Destruction and fragmentation of mature forests in the mountains and Coastal Plain of South Carolina is also a major threat to Rafinesque's big-eared bats and southeastern bats because they depend on these areas for foraging and roosting (Bunch et al. 2015*b*).

Additionally, forestry management practices using a shorter rotation with altered composition of tree species can eventually create a less complex, relatively uniform overstory and a denser understory (Guldin and Emmingham 2007). Management that allows for variation in tree densities (Patriquin and Barclay 2003) as well as a diverse array of herbaceous and woody plants could play a positive role in bat species richness by providing important habitat necessary for the development of prey species consumed by bats such as Rafinesque's big-eared bats (Dodd et al. 2008, Lacki and Dodd 2011).

Forestry practices may also impact some of the most sensitive natural habitats in the state such as caves, sinkholes, and springs (SCFC 2010). These environments are important areas for bats as they provide hibernacula and, especially during periods of drought, key water resources.

Prescribed fire during cold weather may also pose a threat as eastern red bats (Mager and Nelson 2001) and other lasiurine bats are known to use leaf litter during hibernation (Hein et al. 2005, Moorman et al. 1999, Mormann and Robbins 2007, Rodrique et al. 2001). If prescribed burns are conducted during colder winter periods (e.g < 60°F (15°C)), bats roosting beneath leaf litter may be in deep torpor and less likely to escape approaching flames then during warmer periods when they are in shallow torpor (Perry and McDaniel 2015). Increased wind speed during prescribed fires has been found to decrease latencies of response behavior in torpid red bats, as smoke propelled by wind greatly increases bat awareness (Layne 2009).

Loss of Anthropogenic Roosting Habitat

Anthropogenic structures such as mines, wells, cisterns, buildings, and bridges can provide habitat for many species of South Carolina's bats. However, when these structures are closed, filled in, taken down, or renovated to newer designs, bats may lose important roosting or maternity sites (Clark 1990, Keeley and Tuttle 1999, Sherwin et al. 2009). Mine closures can make a significant impact as destruction of hibernacula is the main factor in population declines of bat species dependent on caves and mines (Humphrey 1978, Sheffield and Chapman 1992). The direct impact of mine closures cause bat mortality if they occur during hibernation. Indirect impacts during non-hibernating periods may force bats such as the federally threatened northern long-eared bat to burn critical fat reserves while searching for new hibernacula (USFWS 2011). Also, human-made structures that more recently took the place of tree hollows as colonial roosts are being lost in some areas of the southeast (Belwood 1992, Clark 1990, Lance 1999).

Loss of Spanish Moss and Palm Fronds

The loss of Spanish moss due to a fungal infection poses a big threat to the roosting habitat of northern yellow bats and Seminole bats. Loss due to fungal infection is a possibility due to an outbreak during the 1960's that caused Spanish moss to be eliminated from many areas of central Florida (Jensen 1982, Smith and Wood 1975). The harvesting of Spanish moss may be a problem for these bat species in some areas. However, the development of synthetic materials replacing the need for Spanish moss may have reduced this threat (Trani et al. 2007). Habitat and roost site loss due to the removal of palm fronds is another potential issue for northern yellow bats, evening bats, and Seminole bats (Bunch et al. 2015*c*, Mirowsky 1997).

Sudden Oak Death

Deforestation of oak (*Quercus* species) from Sudden Oak Death (SOD) disease caused by the plant pathogen *Phytophthora ramorum* may pose a threat to habitats critical to forest-dwelling bats. Though it has not been found in a natural setting to date, this disease was recently detected on nursery stock (Bunch et al. 2015*b*).

Feral Hogs

Feral hogs can negatively alter bat habitat by influencing future overstory composition, reducing tree diversity, decreasing plant cover and surface litter, and changing soil composition and chemistry (Siemann et al. 2009). Hogs could also potentially forage on bats roosting in the leaf litter.

Human Disturbance

Disturbance and vandalism of hibernacula by human activities poses a major threat for hibernating bat species (Caceres and Pybus 1997, Thomas et al. 1990, Tuttle 1979). Along with disturbance during summer maternity periods, these threats are a significant factor in the widespread decline of species dependent on caves and mines (Amelon and Burhans 2006*b*, Humphrey 1975, Sheffield and Chapman 1992). There are numerous reports of roosting and nursery colony abandonment due to excessive disturbance, banding and radiotelemetry studies, and survey and netting operations (Bain 1981, Clem 1992, Watkins 1969). Other examples of human disturbance that have lead to abandonment include vandals, careless cave explorers, blocking caves with rocks, setting guano piles on fire, and turning caves into dump sites (Gore and Hovis 1994, Mount 1986, Rice 1957). Mass die-offs of little brown bats at hibernacula not related to WNS have been associated with vandalism (Gould 1970).

Disturbance to hibernacula causes bats to deplete their fat supplies and abandon caves, such as with the threatened northern long-eared bat (Caceres and Pybus 1997). The loss of energy stores may affect overwinter viability as well as other life history events, such as the lowering of reproductive rates due to bats being significantly smaller during the reproductive period (Reichard and Kunz 2009). Disturbance to maternity colonies may lead adults to inadvertently knock young from the roost in their haste to leave, causing juvenile mortality (Foster et al. 1978, Hermanson and Wilkins 1986).

Climate Change

Global climate change is a potential threat to bat species due to the predicted rise in regional temperatures (IPCC 2012). Bats depend highly on temperature for important life history processes such as hibernation, reproduction, and growth, so a change in climate could potentially cause earlier hibernation emergence, extended foraging seasons, and earlier birth of young (Jones et al. 2009).

Bat habitat is also threatened through drought and heat stress associated with climate change (Allen et al. 2010, Hanson and Weltzin 2000, Rennenberg et al. 2006), which has the potential to cause increased tree mortality, insect outbreaks and wildfire. Additionally, roost sites may change as the shift in temperature and precipitation patterns predicted by various climate models alters vegetation (Ayres 1993, Prentice et al. 1991). These changes may make habitat unsuitable and ultimately modify bat distribution through the shifting of their range, as it has with wildlife in other areas (Loarie et al. 2009, Loeb and Winters 2013, Pörtner and Farrell 2008). Migratory bats may also be negatively affected by habitat degradation from climate change (Robinson et al. 2009). Continued change in temperature and precipitation may also alter the availability of insectivorous prey (Bale et al. 2002, Robinson et al. 2009). Climate change has been documented as negatively affecting songbird populations in this way (Both and Visser 2005, Strode 2003).

Though some climate models predict an increase in violent weather events that could affect bat populations in fragmented habitats, the Intergovernmental Panel on Climate Change (IPCC) report on extreme weather events states a lack of strong evidence to support this (IPCC 2012).

Specifically for hibernating bats in South Carolina, the temperature at southern hibernation sites may become too warm and/or fluctuate too greatly. This threat has the potential to cause bats such as the eastern small-footed bat to deplete energy reserves through more frequent arousal from torpor since it hibernates in areas more susceptible to fluctuations in temperature (Humphries et al. 2002, Rodenhouse et al. 2009). However, the exact role that climate change will play in the state on bats and their habitat is largely unknown due to climate model limitations and inadequate experimental data. But if prolonged drought conditions occur, the recruitment of tree species specific to wetlands and bottomland hardwoods would be impacted, and those lands may also become more susceptible to conversion and development (BCI and SBDN 2013).

Wind Energy Development

Wind turbine facilities are a threat to many bats as an estimated 450,000 bat fatalities occur at these locations annually in North America (Ellison 2012). This threat can come from direct mortality caused by either blade strikes or through barotrauma where a sudden change in air pressure near the blades causes damage to lung tissues of bats (Baerwald et al. 2008, Kunz et al. 2007). In addition, habitat loss and fragmentation is associated with construction of these facilities (Arnett et al. 2007). Wind turbine facilities in North America have been increasing in recent years and are expected to continue as the demand for energy increases and fossil fuels become less popular due to sustainability issues, environmental impacts, and wildlife concerns (Arnett et al. 2008, Inkley et al. 2004, Kuvlesky et al. 2007). Wind turbines are a relatively new threat, and thus very little research has been conducted on how to minimize the dangers of turbines to bats. What is known is that the new larger, taller turbines have decreased mortality in birds but actually increased bat fatalities (Arnett et al. 2008, Barclay et al. 2007), and that facilities built on ridge tops appear to have the highest bat fatalities (Johnson and Erickson 2008). In fact, many of the highest mortalities reported come from wind energy sites on forested ridges in the eastern US at 15 to 41 bats killed per megawatt per year (Kunz et al. 2007). Also, estimates of mortality from wind turbines are likely underestimated due to the challenge in finding all carcasses, and the impact from these fatalities may have a cumulative effect on bat populations due to their low reproductive rates.

The majority of wind turbine related deaths is composed of migratory bat species such as eastern red bats, hoary bats, and silver-haired bats, especially during later summer and early fall (Ellison 2012). Hoary bat fatalities are the most prevalent and compose about half of the 450,000 annual bat fatalities at wind facilities in North America, while silver-haired bat mortalities compose about one-fifth of that estimate (Cryan 2011, Ellison 2012). Eastern red bats are also often one of the top species recorded with the most bat fatalities (Ellison 2012). Fiedler (2004) found that 61.3% of the bat fatalities at a wind farm in eastern Tennessee were eastern red bats. The reason wind energy poses a larger risk to migratory bats is likely due to seasonality and migration patterns that make them more vulnerable to collisions (Cryan 2011), such as the use of ridge tops by bats during migration (Johnson and Erickson 2008).

Though the percentages of direct fatalities are low compared to migratory tree bats, wind energy also threatens other species found in South Carolina including tricolored bats, Brazilian free-tailed bats, northern long-eared bats, small-footed bats, little brown bats, and big brown bats. Wind turbines pose a threat to tricolored bats, especially if erected near roosts, colony sites, and along migratory pathways, as mortalities have been reported at multiple wind-energy facilities in the US (Ellison 2012). This species is frequently killed by wind turbines, and deaths may account for up to 25% of total bat deaths (Arnett et al. 2008). Piorkowski and O'Connell (2010) showed a steady rate of collision mortality of Brazilian free-tailed bats at the Oklahoma Wind Energy Center, and reported that of the seven bat species killed by wind turbines, 85% of all bat fatalities were Brazilian free-tailed bats. Wind energy development also threatens northern long-eared bats through direct mortality and the clearing of mature forests for turbines and road construction (Johnson 2005, Kerns and Kerlinger 2004). Because the eastern small-footed bat tends to roost in talus areas occurring on ridge tops, wind power development may adversely affect this species through habitat loss from construction as well (Amelon and Burhans 2006*a*). Little brown bats and big brown bats comprise a small percentage of total fatalities at wind energy developments in the US compared to other species, with little brown bats comprising 5.9% and big brown bats only 1.9% (Johnson 2005). No reports of southeastern bat mortalities by wind turbines have yet been reported, but since other *Myotis* species have been affected, this species may be vulnerable if wind facilities are built near their colonies. The effects of potential off-shore wind farms on bats such as the northern yellow bat are unknown.

No wind turbines have been placed in South Carolina to date, however, Clemson University is constructing a test facility for turbines at the coast (Bunch et al. 2015*b*). Also, areas of the southeast have ideal wind development areas including high-elevation mountain tops, plains, and coastal areas, and Federal Aviation Administration databases indicate numerous proposals for wind energy development across the southeast (BCI and SBDN 2013). It is possible to reduce bat mortality from wind energy by feathering turbine blades (turning them parallel to the wind, affectively idling them) and increasing the cut-in speed. In a synthesis of studies on reducing bat fatalities at wing energy facilities, Arnett et al. (2013) reported that when turbine cut-in speed was increased between 1.5 and 3.0 m/s there was at least a 50% reduction in bat fatalities, and that feathering resulted in up to 72% less bat mortality when turbines produced no electricity for the power grid. In fact, 17 members of the American Wind Energy Association have recently recognized this and volunteered to idle turbines at low wind speeds during peak migration season, potentially reducing bat fatalities at wind farms by 30% (Curry 2015)

Environmental Contaminants

There is increasing evidence that a considerable factor in the decline of bats is exposure to environmental contaminants (Clark 2001, Gerell and Lundberg 1993, Hickey et al. 2001). Pesticide poisoning, especially by organochlorines and anticholinestrase, has been shown to cause population declines in insectivorous bats (Brady et al. 1982, Geluso et al. 1976, Reidinger 1976). Pesticides on forested public lands can cause mortality to both bats and their prey (Bolster 2005). For example, when applied for control purposes they can cause direct mortality to little brown bats, or indirect mortality through their insect prey (Kunz et al. 1977). Pesticides can also alter bat behavior and be transferred to nursing young (Clark 1986, 1981, Henny et al. 1982). Additionally, bats may suffer a delayed affect when high levels are released from stored fat deposits metabolized during weaning, migration, or at the end of hibernation (Bennett and Monte 2007, Geluso et al. 1976). Bat species that consume large amounts of crop pests may have an increased risk of contamination from the accumulation of organochlorine pesticides in body fat. For example, population declines of the Brazilian free-tailed bat reported over the last 50 to 100 years in the US may partially be due to direct or indirect poisoning by pesticides and heavy metals (Gannon et al. 2005, McCracken 1986). Rafinesque's big-eared bat may also be vulnerable to pesticides given the reliance this species has on moths (Hurst and Lacki 1999, Lacki and LaDeur 2001). Potentially, deforestation from gypsy moths (*Lymantria dispar*) and/or control measures for gypsy moths, such as broadcast usage of *Bacillus thurinigiensis* var. *kurstaki* may impact Rafinesque's big-eared bats (Bunch et al. 2015*b*).

Contaminants of emerging concern, such as flame retardants, pharmaceuticals and personal care products, have been discovered in high concentrations in bats. A recent study by Secord et al. (2015) found that out of 48 bat carcasses collected in the northeastern US, 100% showed high detection frequencies of polybrominated diphenyl ethers (PBDEs), or flame retardants, in their system. Also in relatively high detection frequencies were salicylic acid (81%), thiabendazole (50%), caffeine (23%), and in at least 15% were compounds such as ibuprofen, penicillin V, testosterone, and DEET. Though it is not known how these chemicals affect bats, it is possible that they could make them more susceptible to WNS, or in the case of caffeine, arouse bats out of hibernation prematurely.

Elevated levels of contaminants such as heavy metals like mercury have been found in bats, and can be toxic in high concentrations. In a South Carolina study on Rafinesque's big-eared bats, Bennett et al. (2003) found elevated levels of Al, Cd, Cr, Cu, Hg, Ni, Pb, and Zn in all hair samples measured, and As and Se in the majority of samples. The Al (aluminum) concentrations in hair samples were an order of magnitude higher than those found in little brown bats in Ontario and Quebec. Other concerning results were the levels of Pb (lead) and Hg (mercury), which are considered highly toxic to wildlife. Of the samples measured, 24 % had an amount of lead greater than the lower limit considered toxic. Even worse, 55% of the samples had mercury near or above the level at which detrimental effects have been recorded in humans and rodents. Many bats, such as the silver-haired bat, may be particularly vulnerable to heavy metal contamination due to their tendency to forage over water. Eastern small-footed bats may also be particularly vulnerable to environmental contaminants due to their small body size and association with mining activities (Amelon and Burhans

2006*a*). Waterways in South Carolina with mercury and PCB advisories can be seen at http://www.scdhec.gov/FoodSafety/Docs/FISH2015.pdf

Other Threats

Inadequacy of Existing Regulations

The inadequacy of existing regulations for the management of forestry, wind energy development, and oil, gas, and mineral extraction when it comes to the protections afforded a state-listed species is another potential threat to South Carolina's bats. These protections are meant to prevent trade or possession of state-listed species, but do not to protect against habitat destruction (USFWS 2011).

Collisions from Buildings

Large buildings also pose a collision threat to some migratory species such as eastern red bats (Timm 1989). Additionally, small numbers of deadly collisions with towers in Florida have been recorded for Seminole and southeastern bats (Crawford and Baker 1981). In South Carolina, the carcass of a hoary bat that hit a power line exists at the Campbell Museum of Natural History. However, the level of impact from tower or building mortalities on local or range-wide populations is a relatively minor threat.

Current Conservation, Management, and Outreach Activities

Surveys and Research

Past and Current Surveys and Research

One of the earliest comprehensive reports on the species, distribution and natural history of 11 of the 14 bats in South Carolina was provided in a general mammal survey of the state by Golley (1966). That information was updated by Neuhauser and DiSalvo (1972) with the first record of a southeastern bat in the state, new county records for other bats, and expanded ranges for Seminole and Brazilian free-tailed bats. Using bats submitted for rabies testing, DiSalvo et al. (2002) further updated these bat species distributions. One year later, Menzel et al. (2003) contributed additional information to the South Carolina bat distribution maps from museum records, captures reported in literature, and records maintained by SCDNR.

Most research specifically investigating natural history of South Carolina bats did not begin until the late 1980's. Results from these early bat surveys exist in internal documents but are reflected in the Campbell Museum of Natural History records at Clemson University. Available studies from the late 1990's ranging from topics on diet, roosting habits, foraging habits, and species prelisting recovery come in the form of survey reports (Bunch and Dye 1999*a*, *b*, Bunch 1998, Bunch et al. 1998*a*, *b*, 1997, Cothran et al. 1991, Louie et al. 2001), unpublished master's theses (Carter 1998, Menzel 1998), and an honors project (Donahue 1998).

Between 2000 and 2003, a large portion of bat research was conducted in the Sandhill ecoregion at the U.S. Department of Energy's Savannah River Site on 12 of the 14 bat species of South Carolina (Menzel et al. 2003*b*, 2002*a*, *b*, 2001*a*, 2000*b*). These studies focused on foraging ecology, tree roost selection, home range, habitat use, diet, and spatial activity patterns. Since 2003, research studies on specific bat species and communities in various regions of the state have been conducted on bat activity (Hein 2008, Loeb and Waldrop 2008, Menzel et al. 2005*a*), community and social structure (Loeb and Britzke 2010, Loeb et al. 2009), diet (Armbruster 2003, Carter et al. 2004), presence and absence (Ford et al. 2006*a*), habitat use (Loeb and O'Keefe 2006), roost site selection (Bennett et al. 2008, Hein et al. 2008*a*, 2005, Leput 2004, Loeb and Zarnoch 2011), variation in metal concentrations (Bennett 2004), and the presence or absence of rare, threatened, and endangered species (Webster 2013). Current studies include research lead by Susan Loeb on foraging and roosting habitat of southeastern bats at Congaree National Park and an ongoing study on band injury rates of big brown bats. The master's thesis of Lydia Moore researched the selection of wetland habitat by bats in coastal South Carolina using acoustic detectors, the final results of which should become available in late 2015.

South Carolina bat surveys are generally conducted by SCDNR and the USFS. SCDNR has conducted multiple surveys at the Army National Guard's McCrady Training Center (previously known as the Leesburg Training Site) in the Sandhills ecoregion of the state (Bunch et al. 1998*b*, 1997) and the Naval Facilities Engineering Command in the Coastal Zone ecoregion (Bunch 1998, Louie et al. 2001). Winter hibernacula counts in the Blueridge and Piedmont ecoregions are the largest ongoing surveys and are conducted on a three to five year rotation by SCDNR. The USFS Southern Research Station has been conducting annual winter counts at the Clemson University owned railroad tunnel for the past three years.

The most information collected on a single species in South Carolina thus far has been on Rafinesque's big-eared bat. This is probably due to its long standing status as state endangered, and the fact that relative abundance and distribution of the species are not easily estimated due to capture and detection challenges.

Habitat and Species Protection

Lands protected in South Carolina by federal, state, or nonprofit conservation organizations conserve a total of 11% of the state. Overall conservation acreages in the state include 469,000 (190,000 ha) for state-owned, 990,000 (400,000 ha) for federally owned, 671,000 (272,000 ha) for privately owned, and 91,000 (37,000 ha) for military owned lands (SCDNR 2015*a*). The Blue Ridge ecoregion has the greatest percentage of land conserved at 57%, where approximately 163,000 acres (66,000 ha) are protected by preserves, conservation easements, and national forests such as Ashmore Heritage Preserve, the South Saluda watershed of the Greenville Water System, the Andrew Pickens District of Sumter National Forest, and the Mountain Bridge Wilderness Area (Bunch et al. 2015*b*). For the other ecoregions, 29% of the Coastal Zone, 14% of the Sandhills, 10% of the Coastal Plain, and 6% of the Piedmont at 6% are protected (SCDNR 2015*a*). In terms of the largest number of acres protected, the Coastal Plain is responsible for 39% of South Carolina's conserved land, with federal lands and public ownership playing major role in habitat protection. In this ecoregion, Congaree National Park encompasses nearly 27,000 acres (10,926 ha) and is the largest old growth bottomland hardwood forest in the southeastern US. Also, Francis Beidler Forest, owned by the Audubon Society, protects 16,000 (6,475 ha) acres of old-growth swamp.

As mentioned in the Legal and Conservation Status section of this document, bat species are protected on Heritage Preserves and SCDNR owned lands (CL 50-11-2200 (C), Appendix A). The Heritage Trust Program protects critical natural habitats and significant cultural sites in heritage preserves, and identifies conservation ranks for South Carolina bat species according to NatureServe criteria (Table 2). The Heritage Trust Program also maintains a database with current and historical bat data that's been collected in the state. Other SCDNR habitat protection programs include the Forest Legacy Program, Focus Area Program, ACE Basin Project, Scenic Rivers Program, South Carolina Conservation Bank Act, National Estuarine Research Reserve System, South Carolina Land Trust Network, and Beach Sweep/River Sweep (SCDNR 2015*a*).

Conservation Plans and Recommendations

The South Carolina SWAP identifies 12 of the 14 bats in the state as species of conservation concern or greatest conservation need (Table 2) (SCDNR 2015*a*). Conservation recommendations for these species are provided in the Supplemental Volumes of the plan and titled Colonial Cavity Roosting Bats Guild, the Foliage Roosting Bats Guild, and Silver-haired Bat (Bunch et al. 2015*a*, *b*, *c*). These recommendations include specific information for management, priority research and survey needs, monitoring, education, public outreach and cooperative efforts in South Carolina.

"A Conservation Strategy for Rafinesque's Big-Eared Bat (*Corynorhinus rafinesquii*) and Southeastern Myotis (*Myotis austroriparius*)" (BCI and SBDN 2013) is an extremely detailed plan developed to help guide conservation and management of these South Carolina bat species. Also, the symposium on the "Conservation and Management of Eastern Big-eared Bats" (Loeb et al. 2011) is particularly useful for information regarding the conservation needs and management of Rafinesque's big-eared bats. The "Conservation Assessments for Five Forest Bat Species in the Eastern United States" consolidated and synthesized by the USFS (Thompson 2006) provides conservation information for the southeastern bat, eastern small-footed bat, northern long-eared bat, tricolored bat, and evening bat. In this document, potential threats, estimates of habitat availability, and percentages of protected habitat available within the National Forest System are outlined. Additionally, estimates of habitat availability are shown in the form of acreage across ownerships, such as federally owned, State-owned, county or municipal-owned, and privately owned lands.

Educational Outreach

Current Informational and Bat Management Materials

Informational materials on South Carolina bats are largely provided by SCDNR. The department contributed to a major educational outreach tool, the "Bats of the Eastern United States" bat identification poster, which is provided for free to the public. Other materials can be accessed on the SCDNR website, and the following are descriptions and links to these documents.

SC bats in buildings - written specifically for the public, this document provides information on the bats of South Carolina, how to safely exclude them from structures and living quarters, and provides links on how to build bat boxes and report South Carolina bat colonies. http://www.dnr.sc.gov/wildlife/publications/nuisance/SCbatsinbldgs.pdf

Bats and White Nose Syndrome (WNS) - this webpage describes WNS, why it's a problem, what SCDNR is doing about it, and what the public should do if a dead bat is found. It also provides links to the recently updated South Carolina WNS response plan, a document on the Bats of the Southern Appalachians, an informative USFS video, and additional information on WNS. http://www.dnr.sc.gov/wildlife/batswns.html

The South Carolina SWAP link provides the entire action plan for the state: http://dnr.sc.gov/swap/index.html. Bat species information in the SWAP is found under the Supplemental Volume, Mammals section. For the Colonial Cavity Roosting Bats Guild: http://dnr.sc.gov/swap/supplemental/mammals/colonialcavityroostingbatsguild2015.pdf
For the Foliage Roosting Bats Guild: http://dnr.sc.gov/swap/supplemental/mammals/foliageroostingbatsguild2015.pdf
For the Silver-haired Bat: http://dnr.sc.gov/swap/supplemental/mammals/silverhairedbat2015.pdf

The Rare, Threatened and Endangered Species Inventory link lists these species in South Carolina by county: http://www.dnr.sc.gov/species/index.html

Bat Conservation Organizations

National and Regional Levels

A major player on the national level of bat conservation is Bat Conservation International (BCI), a non-governmental organization that works to conserve the world's bats and their ecosystems. In the US, they have conducted research and conservation activities in order to protect habitat, mitigate threats to bats, and educate the public. Specifically, they help safeguard critical bat colonies in Texas and Alabama, address the threat of wind energy and water scarcity for bats, and provide resources and funding toward WNS recovery efforts. On the regional level, the Southeastern Bat Diversity Network (SBDN) helps to conserve bats and their habitats as well as facilitate education, research, and management in the Southeast. This working group is composed of bat biologists, land managers and others from 16 southeastern states seeking to facilitate communication, identify bat conservation priorities, and implement conservation programs regionally. Together, BCI and SBDN created the Conservation Strategy for Rafinesque's Big-Eared Bat (*Corynorhinus rafinesquii*) and Southeastern Myotis (*Myotis austroriparius*) (BCI and SBDN 2013).

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 T. H. 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% (Frick et al. 2010*b*, 2007, O'Shea et al. 2011, 2010, Tuttle and Stevenson 1982).

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 the high frequency sounds bouncing off of 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 (Barclay 1999, Fenton 1990, Neuweiler 1989). 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. In order 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 (Lacki et al. 2007, Schnitzler and Kalko 1998). 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 off of 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 4, 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

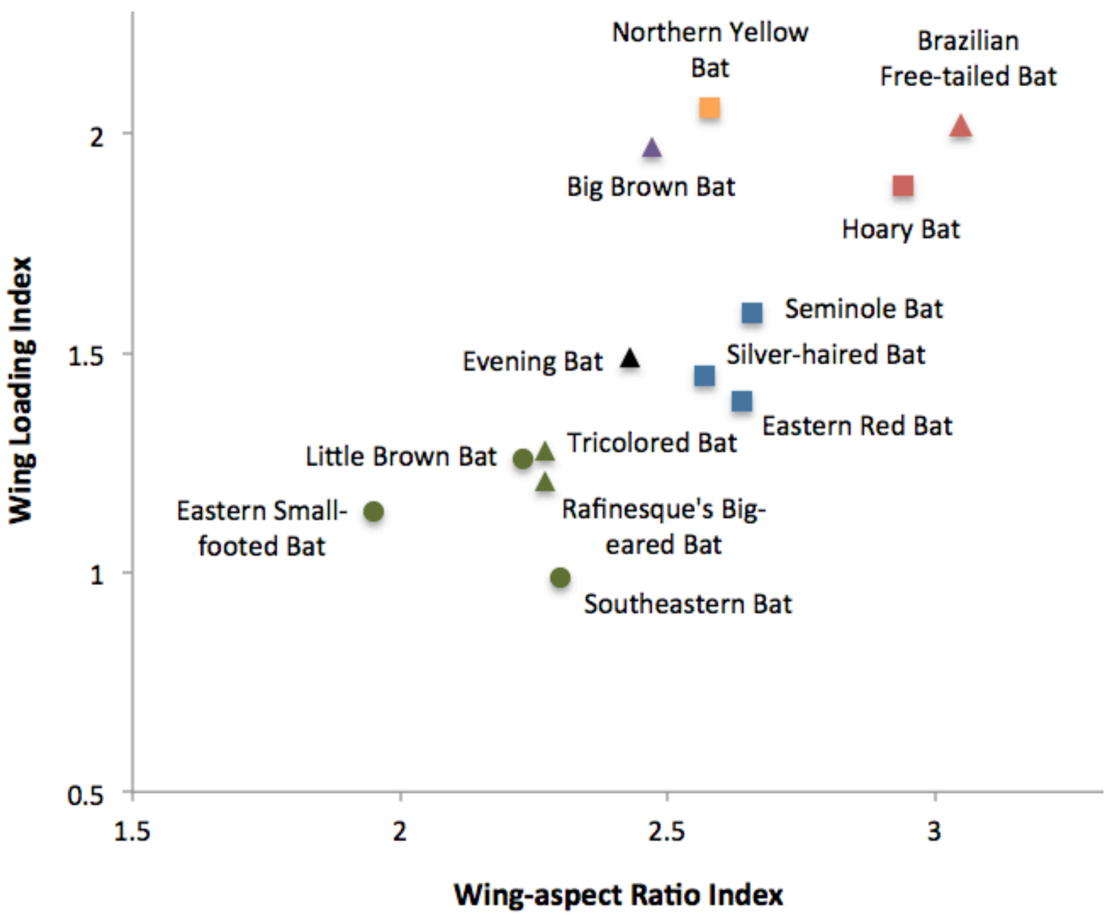

Figure 4: Wing loading and aspect ratios of southeastern bats. All calculations from bats captured at the Savannah River Site by Menzel et al. (2003) except eastern small-footed bat which came from Johnson et al. (2009). No information was provided for northern long-eared bat. Circles = colonial roosting *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.

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 4, colored in yellow), while the eastern red bat, Seminole bat, and silver-haired bat fly at relatively slower speeds (Figure 4, 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 4, 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*a*), 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 4, colored in black), and despite its general classification as a clutter-adapted species, tends to forage above the forest canopy, in forest gaps, clearcuts, young tree stands, or over water in South Carolina (Menzel et al. 2005*a*, 2003*b*, 2001*a*).

Diet

In the southeastern US, at least 12 dietary studies of bats have been conducted. Nearly half of those were in Florida (Jennings 1958, Sherman 1939, 1935, Zinn and Humphrey 1981, Zinn 1977), 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*a*). 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, Kunz et al. 1995, Kurta et al. 1990, 1989*a*). 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.

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

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 (Altringham 2011, Geiser 2010). 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) (Padgett and Rose 1991, Reite and Davis 1966, Whitaker et al. 1997).

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 (Geiser 2004, Grinevitch et al. 1995, 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, Chruszcz and Barclay 2002, Grinevitch et al. 1995, 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, Rambaldini and Brigham 2008, Willis 2006).

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 Mumford 2009, Whitaker and Rissler 1992*a*), northern yellow bat (Jennings 1958), Seminole bat (Wilkins 1987), and silver-haired bat (Dunbar 2007, Falxa 2007, Humphrey 1975, Nagorsen and Brigham 1993). 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 (Ferrara and Leberg 2005, Jones and Suttkus 1975). 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 (Fujita and Kunz 1984, Griffin 1940, 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 it's body weight during winter in the northern portions of its range (Caceres and Barclay 2000, Caire et al. 1979). 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 (Altringham 2011, Luis and Hudson 2006, Ransome 1990, Thomas and Geiser 1997). 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 (Briggler and Prather 2003, Whitaker and Rissler 1992*b*). 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) (Amelon 2006, Twente et al. 1985).

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 (Clark et al. 1987, Jones et al. 1967), 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 (Hein 2008, Menzel et al. 2001*a*), 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*, Menzel et al. 2003*b*, 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 are able to 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 (Menzel et al. 2003*b*), northern long-eared bats in a cave and single individuals in tunnels (Bunch 2011, Bunch et al. 1998*a*), 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 (Menzel et al. 2003*a*).

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 (Brenner 1968, Davis 1967, Mills et al. 1975) have high fidelity to maternal roosts, and eastern small-footed bats (Gates et al. 1984), northern long-eared bats (Caire et al. 1979, Griffin 1945, Mills 1971), 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, Mager and Nelson 2001, Menzel et al. 1998). Frequent roost switching may be a response to changing microclimate conditions at different trees (Hoffmeister and Goodpaster 1963, Jones and Suttkus 1975, Kunz 1982*b*, McNab 1974). 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 (Cryan et al. 2001, Elmore et al. 2004, Lunney et al. 1988).

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 in order 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 (Menzel et al. 2003*b*). 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 (Menzel et al. 2003*b*). 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 actually 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 (Arnett et al. 2008, Barclay 1984, 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 (McGuire et al. 2012, Reimer et al. 2010). 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 (Bunch et al. 2015*a*, Menzel et al. 2003*b*), 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 (Cryan et al. 2001, Elmore et al. 2004, Lunney et al. 1988, 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 features like nearby foraging areas and water resources may also play a part in roost selection by bats.

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

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 (Altringham 2011, Sherwin et al. 2009, Tuttle and Taylor 1998). 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 48 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 (Menzel et al. 2003*a*). 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 (Altringham 2011, Rancourt et al. 2005). 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 (Maser 1998, Nagorsen and Brigham 1993).

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 (Kalcounis-Ruppell et al. 2005, Menzel et al. 1998), 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 Brigham 1998, Kalcounis and Hecker 1996, Mattson et al. 1996, Vonhof and Barclay 1996). 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*b*). 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 of the *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, 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 (Crampton and Barclay 1998, Kalcounis and Hecker 1996). Northern long-eared bats roost in tree cavities (Menzel et al. 2002*d*, Owen et al. 2001) 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 (Caceres and Barclay 2000, Foster and Kurta 1999, 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 (Caceres 1998, Sasse and Pekins 1996), in live trees with less canopy closure (Caceres 1998), and in large diameter trees (Foster and Kurta 1999, Sasse and Pekins 1996). 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 (Carver and Ashley 2008, Cochran 1999, Hoffman 1999), 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*) (Bat Conservation International 2015, BCI and SBDN 2013, Reed 2004, Stevenson 2008, Wilf 2004). 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 (Humphrey 1992, Rice 1957). 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 (Carver and Ashley 2008, Gooding and Langford 2004, Mirowsky 1998, Trousdale and Beckett 2005). 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 (Cryan et al. 2001, Elmore et al. 2004, Lunney et al. 1988). 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*b*). 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 (Barbour and Davis 1969, Constantine 1958, 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 (Constantine 1966, Cowan and Guiguet 1965, Neill 1952). Northern yellow bats have been found roosting in Spanish moss in live oaks (*Quercus virginiana*) in Georgia and Florida (Coleman et al. 2012, Jennings 1958, Menzel et al. 1995), in pine-oak woodlands in Florida and Mexico (Carter and Jones 1978, Jones 1964, Sherman 1944), 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 (Barbour and Davis 1969, Constantine 1958, Jennings 1958), but also in the canopy of live pine trees (Menzel et al. 2000*b*, 1999*a*, 1998, 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*b*). 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 (Betts 1998, Campbell et al. 1996, Mattson et al. 1996) and old-growth forests (Jung et al. 1999, Thomas 1988). 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 (Betts 1996, Mattson et al. 1996, Parsons et al. 1986, 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 (Mattson et al. 1996, Parsons et al. 1986, 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 1991, 1990), 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*a*), 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*a*).

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 (Ford et al. 2006*a*, Menzel et al. 2005*a*, 2003*b*). 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 1999, Hoffman et al. 1998). 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 (Barclay 1985, Nagorsen and Brigham 1993, Shump and Shump 1982*a*). 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 (Harvey et al. 1999*a*, Linzey 1998, Merritt 1987), 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 (Ford et al. 2006*a*, Menzel et al. 2005*a*, 2003*b*). Mature forests, mature deciduous uplands, and mature forested wetlands are also important roosting and foraging habitats for bats, especially northern long-eared bats (Caceres and Pybus 1997, Kunz 1973, 1971) and southeastern bats (Gardner 2008, Gardner et al. 1992, Horner 1995). 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.