

FINAL REPORT
South Carolina State Wildlife Grant SC-T-F17AF01195
South Carolina Department of Natural Resources
October 1, 2017 – December 30, 2020

* *This grant was awarded a 6-month extension to December 30, 2020 for reporting purposes.*

Project Title: South Carolina Bat Monitoring and Research Project

The purpose of this grant was to determine overall bat species richness and opportunistically radio-track federally threatened bat species on state-owned or conservation partner-held properties; continue achieving our long-term White-nose Syndrome (WNS) goals through WNS surveillance and outreach; determine roosting requirements and foraging area characteristics of Northern Yellow Bats and Northern Long-eared Bats on the Lower Coastal Plain of South Carolina (SC); initiate a SC Citizen Science Bat Watch program; and to create a South Carolina Department of Natural Resources (SCDNR) bat database to efficiently house and share bat data.

The SCDNR bat biologist was assisted by a WNS hourly technician, funded by *SC-E-F17AP00633 SC White-nose State Support in 2017* and *SC-E-F18AP00557 SC White-nose State Support in 2018*, with additional netting and WNS-related duties. This report includes those shared activities, but details of specific WNS-related duties can be found in the final report for those grants.

Objective: Conduct bat netting and trapping across the state to identify locations of federally threatened bat species and determine bat species richness on state-owned or conservation partner-held properties.

Accomplishments:

A total of 269 bats representing 10 different species were captured by SCDNR during the 2018 and 2019 summer netting seasons (Table 1). This included 8 Northern Long-eared Bats (*Myotis septentrionalis*, MYSE; federally threatened) captured on the coastal plain: 2 subadults (1 male, 1 female), 3 adult males, and 3 pregnant females. A total of 5 of these individuals were tracked to day roost sites: both subadults (1 male, 1 female), 1 adult male, and 2 pregnant females. See Appendix A for a more details on these tracking and day roost surveys. Our efforts in 2019 marked the first time pregnant MYSE have been captured on the South Carolina Coastal Plain since the species was discovered in Beaufort County in 2016. We estimate the pup season for this population to be between late April and early May, approximately one month earlier than the June 1 – July 31 pup season outlined by the [US Fish and Wildlife Service](#) in the current 4(d) Rule.

Mist Netting Surveys

SCDNR conducted bat netting surveys between May 21 and July 10 in 2018, and April 15 and June 14 in 2019. In order of most bats captured (Table 1), the properties netted were: Santee Coastal Reserve Wildlife Management Area (WMA)/Washo Reserve, Belfast WMA, Chestnut Ridge Heritage Preserve (HP), Lewis Ocean Bay HP, and Stumphouse Mountain HP. Washo Reserve is owned by The Nature Conservancy and exists within Santee Coastal Reserve WMA. For simplicity, we refer to the entire site as Santee Coastal through the rest of this document. Santee Coastal and Lewis Ocean Bay HP are located on the coastal plain and within the recently expanded range area for MYSE. Chestnut Ridge and Stumphouse Mountain HPs are within the historic, previously known range for MYSE in the Blue Ridge

ecoregion. Belfast WMA is in the Piedmont ecoregion, in between the historic mountain range and currently known coastal range of MYSE of SC.

Netting effort resulted in 404 nets (also referred to as net nights) deployed over 48 total survey nights for a total of 269 bats captured representing 10 species (Table 1). A total of 8 MYSE were captured on the coastal plain, all at Santee Coastal: 2 subadults (1 male, 1 female), 3 adult males, and 3 pregnant females. For any site in one season, the number of net nights ranged from 87 to 44 and number of individuals from 83 to 5. During the two-year period, capture rate per net night of effort (total number of bats captured divided by total number of nets) is listed from highest to lowest site as follows: Santee Coastal: 0.97; Belfast WMA: 0.96; Chestnut Ridge HP: 0.52; Lewis Ocean Bay: 0.28; and Stumphouse Mountain HP: 0.11. Species richness was also highest at Santee Coastal (9 species) and lowest at Stumphouse Mountain HP (3 species). Thus, Santee Coastal had the highest capture rate per night, highest species richness, and was the only site with MYSE present. This site also accounted for 83% of all *Myotis* species captured overall (all MYSE and Southeastern Bats (*Myotis austroriparius*; MYAU)), with Chestnut Ridge HP accounting for the other 17% (MYLE). Lastly, Santee Coastal accounted for 90% of the Tri-colored Bats (*Perimyotis subflavus*, PESU) captured, with Belfast WMA and Chestnut Ridge accounting for the other 10% of total captures (1 PESU each).

Of note was the Seminole Bat (*Lasiurus seminolus*, LASE) captured in Oconee County in 2018. There are a total of 5 records of LASE in the Blue Ridge ecoregion, all of which were documented in 2017 and 2018, suggesting that the range of LASE is expanding in SC. Also observed was the reduced capture rate of PESU and MYAU at Santee Coastal in 2019 compared to 2018 despite similar netting effort. Only 2 PESU and 5 MYAU were captured, representing an 86% and 58% reduction in capture rates, respectively. Though both species are affected by WNS, especially PESU in more northern portions of its range, this difference could be a result of differing habitats netted across years. In 2018, approximately 50% more of the net sites were in cypress swamp compared to the mature hardwood near marsh or a pond netted in 2019. However, the 2019 netting sites were 2 miles or less away from those in 2018, and all 2019 sites were still near water.

Radio-tracking Surveys

Two subadults, 1 adult male, and 2 pregnant female MYSE were fitted with radio transmitters and tracked to day roost sites. A sweetgum (*Liquidambar styraciflua*) cavity within 300 feet of the capture location was used by the adult male for at least 5 days. All females roosted under bark of live, mature longleaf pine (*Pinus palustris*) within 150 feet of a road, in uniform aged stands approximately 85 years old undergoing frequent fire (1 to 5 years) and managed for local populations of endangered Red-cockaded Woodpeckers (*Leuconotopicus borealis*). Average female roost tree (n = 10) characteristics were approximately 30% canopy closure, 14-inch DBH, 30% exfoliating bark, and approximately 58 feet tall. All females were found to switch roosts daily, and distances between the previous roost varied between 5 and 1,200 feet. Only one roost tree was used twice. Females generally roosted alone, and no maternity colonies were found. Capture locations for females were about one mile away from their day roosts, and capture site habitat varied greatly from that of day roosts. Females were tracked to longleaf pine roosts from capture sites in either a mixed hardwood pond area (subadult female) or closed canopy near-maritime forest (both pregnant females). We suspect capture sites were primarily foraging areas. We estimate the pup season for this population to be between late April and early May, approximately one month earlier than that outlined in the current 4(d) Rule.

Table 1: Summer mist netting results for 5 total sites in 2018 and 2019. WMA = Wildlife Management Area, HP = Heritage Preserve. Net nights are calculated using the method in the Range-wide Indiana Bat Summer Survey Guidelines.

Location	County	Dates	Net Sites	Net Nights	Bats ^a									Total
					CORA	EPFU	LABO	LASE	MYAU	MYLE	MYSE	NYHU	PESU	
Santee Coastal Reserve WMA	Charleston	4/15 - 5/3/19	25	87	2	13	23	25	5		5	7	2	82
		5/21 - 6/6/18	25	84		13	14	8	12		3	15	15	3
Belfast WMA	Laurens & Newberry	6/18 - 6/28/18	10	45		7	15					20	1	43
Chestnut Ridge HP	Greenville	5/28 - 6/14/19	12	66		11	17			5			1	34
Lewis Ocean Bay HP	Horry	5/6 - 5/23/19	20	78		1	10	10					1	22
Stumphouse Mountain HP	Oconee	7/2 - 7/10/18	13	44		2	2	1						5
Totals	5	48	105	404	2	47	81	44	17	5	8	43	19	269

^a CORA = *Corynorhinus rafinesquii*, EPFU = *Eptesicus fuscus*, LABO = *Lasiurus borealis*, LASE = *Lasiurus seminolus*, MYAU = *Myotis austroriparius*, MYLE = *Myotis leibii*, MYSE = *Myotis septentrionalis*, NYHU = *Nycticeius humeralis*, PESU = *Perimyotis subflavus*, TABR = *Tadarida brasiliensis*

Swabbing for the *Pseudogymnoascus destructans* (or *Pd*, the fungus that causes WNS) was conducted both years, and results were negative for the fungus. See Appendix A for a more detailed report of Northern Long-eared Bat tracking and day roost surveys at Santee Coastal Reserve WMA in 2018 and 2019.

Significant deviations:

There were no significant deviations.

Objective: Conduct WNS-related bat duties such as WNS surveillance and WNS outreach.

WNS surveillance

Full results of WNS-related duties can be found in the *SC-E-F17AP00633 SC White-nose State Support in 2017* and *SC-E-F18AP00557 SC White-nose State Support in 2018* final reports, which funded the WNS hourly technician to assist with these duties. What follows is a summary of the combined efforts by the SCDNR bat biologist and WNS technician.

In the winters of 2018 and 2019, a total of 30 hibernacula counts were conducted in caves, mines, rock shelters and culverts. We recorded a total of 154 PESU, 3 EPFU, 2 Eastern Small-footed Bats (*Myotis leibii*, MYLE), and 1 Rafinesque’s Big-eared Bat (*Corynorhinus rafinesquii*, CORA). Of all the bats observed, only 5 PESU at 2 sites in Oconee County (WNS confirmed in 2014) were seen with white fungal growth on the face and ears, indicative of WNS. No other bats were observed with obvious clinical signs of the disease. National Wildlife Health Center (NWHC) swabbing for the *Pd* was conducted, and results indicated that *Pd* was present on PESU in 3 new counties: Cherokee, York, and

Spartanburg. These counties are now considered WNS suspect. A WNS sign was posted at the Spartanburg site determined to have *Pd* present (Hammet Mine). The owner of two sites found to have *Pd* present was also offered these signs but declined.

In early spring at Santee Coastal in 2018 and 2019, swabbing using NWHC spring trapping kits was conducted. Total individuals swabbed included 17 PESU; 17 MYAU; 15 Evening Bats (*Nycticeius humeralis*, NYHU); 8 LASE; 25 Big Brown Bats (*Eptesicus fuscus*; EPFU); 14 Eastern Red Bats (*Lasiurus borealis*, LABO); 3 Brazilian Free-tailed Bats (*Tadarida brasiliensis*; TABR); and 8 MYSE. Two additional environmental samples and 15 guano pellets were also collected for testing. No visible fungus or mortality was noted in the bat population at the time of the survey, and no samples tested positive for *Pd*. Note the lack of a positive result by PCR does not definitively indicate the absence of the organism as it may not be detected if it is at very low abundance in the sample.

WNS Outreach

Letters updating over 167 National Wildlife Control Operators (NWCOs) listed as working on bats were distributed on March 21, 2018, September 24, 2018, April 10, 2019, and September 10, 2020 for a total of 551 letters sent. These NWCO letters included information about: newly identified WNS suspect counties in SC, current decontamination information, WNS brochures and updates from the whitenosesyndrome.org, online bat standards course links, and recommended Personal Protection Guidelines (PPE) from the National Wildlife Control Operators Association (NWCOA) in response to concerns regarding potential transfer of COVID-19 from humans to bat populations. See Appendix B for the most recent letter. A grand total of 7 news releases, 18 presentations, 1 interview, 2 articles, 1 newsletter, and multiple social media posts provided WNS outreach and bat information. Over 400 people attended presentations, and Social Media post response was over 538 likes and 132 shares. The SC WNS Response Plan was updated on the [SCDNR WNS website](#) April 4, 2018, Sep 27, 2018, April 11, 2019, July 31, 2019, and September 29, 2020. The SC Bat Conservation Plan was [updated online](#) on April 4, 2018, July 16, 2019, and September 29, 2020. The SCDNR bat biologist participated in monthly WNS partner conference calls and attended Southeastern Bat Diversity Network and WNS meetings in 2018, 2019 and 2020.

Significant deviations:

There were no significant deviations.

Objective: Initiate a Citizen Science Bat Watch Program to monitor bat maternity roosts at various locations across the state.

Accomplishments:

We created the SCDNR Bat Watch Citizen Science Project, a (minimum) twice annual bat emergence count of summer maternity sites, called *SCDNR Bat Watch!* and registered it on www.SciStarter.com. We created various documents for the project including a detailed instruction sheet, a species ID guide, and a one-page summary that also functions as a flyer for distributing. We created a web page (<https://www.dnr.sc.gov/wildlife/bats/batwatch.html>) that contains a full description of the project, links to all the forms and printable documents, an embedded video of a bat emergence to practice with, and information about a Bat Watch training. We also created a *SCDNR Bat Watch!* app based off the datasheet that volunteers can use in the field with the free Survey123 app and added links and instructions on how to use it under the Data Submission section of the SC Bat Watch! website. This makes the project more user friendly, allowing collected data to be entered real time while decreasing

the likelihood of not submitting data afterward. Being able to view the data also helps us target parts of the State not yet being covered by citizen scientists. A Bat Watch window decal was made to distribute to participants as a thank you and as a promotion for the project. To garner interest in the project, we held Bat Watch trainings at Sunrift Adventures Inc., a popular outdoor outfitter and rental business in Travelers Rest, SC. Sunrift has installed 8 bat boxes on their storage building, which collectively house hundreds of bats (TABR and EPFU), creating an impressive bat emergence opportunity that they willingly share with the public. We held two spring trainings, one in 2018 and 2019, with a total of 50 people in attendance. Over 1,000 TABR were counted emerging from the bat boxes, and a projector and screen were set up to show how to download and use the new Survey123 app as part of the training. We had still hoped to hold an additional Bat Watch Training in the spring of 2020 but could not do so due to the COVID pandemic. We also held Halloween Bat Counts in 2018, 2019, and 2020, with a total of 180 people in attendance and 2,200 bats (max was 900 bats in 2019) counted emerging from Sunrift boxes.

Overall, between 2018 and 2020, a total of 135 emergence counts were submitted from bat boxes (128 observations), bat condos (2 observations), buildings (5 observations), and trees (1 observation) by 14 volunteers at 25 sites across the state (Figure 1) for a grand total of 15,621 bats counted. We will continue to advertise *SC Bat Watch!* in bat presentations, news releases, and social media posts including events set up for Bat Watch Training and Halloween Bat Count.

We also collected bat guano from 3 bat roost locations at Oconee State Park and Musgrove Mill State Historic site and sent them to Northeastern Arizona University for bat species identification as part of their Species from Feces Program. Musgrove Mill bat box harbors TABR. Oconee State Park species at the barn bat box were TABR and EPFU while those at the shelter bat box next to the lake were TABR, EPFU and a smaller proportion of Little Brown Bats (*Myotis lucifugus*, MYLU). We have not recorded any MYLU in netting or hibernacula surveys since 2016, so we were excited to hear this species was using a bat box at Oconee State Park. These boxes have been falling into disrepair recently, and knowing that MYLU use it, the State Park service and SCDNR have been working to replace them with rocket boxes in locations a little further away from a major viewshed but with a similar amount of sun.

Significant deviations:

There were no significant deviations.

Objective: Create and manage an SCDNR bat database to efficiently house and streamline data sharing of all bat data from hibernacula counts, summer/fall netting, acoustic data, and citizen science Bat Watch data.

Accomplishments:

We worked with Joe Lemeris, SCDNR Geospatial Analyst, to set up an ArcGIS database and data entry forms into our Heritage Trust database. The new system allows for easy data entry in the field or office using the ArcGIS app Survey123. Previously, all data collected on bats, including hibernaculum counts, mist netting, and other records of occurrence, were entered in Biotics. We now have a Survey123 form to enter our netting data, which was used in the field in 2019 with great success. We also created and used a Survey123 for our hibernacula data and are currently working with partners at North American Bat Monitoring Program (NABat) to improve it to collect specific NABat fields alongside our own SCDNR fields in Survey123 and extract the NABat fields for submission once the data is entered. We hope to do the same with the other NABat Survey123 forms for emergence count data, maternity colony count data, and mobile and stationary acoustic metadata. With the new ease of data entry, we can enter

not only SCDNR collected data but submit data from bat research around the State. We based netting database fields on the US Fish and Wildlife Service (FWS) bat reporting excel spreadsheet required for their permitting process so we can import data already collected by partners for the FWS. This ensures we receive the same bat data as the FWS, and SC state permittees are not required to enter their data twice. Also, in Survey123 there is an option to add images, which is helpful for documenting uncommon species and evidence of WNS-related wing damage. We also created a Bat Data Manager application online to view and edit data submitted. As an important part of database management, this application will allow us to check, edit, and improve the quality of bat data. Bat watch data (see Bat Watch objective) was submitted directly into our SCDNR bats ArcGIS online account. Because it is difficult for citizen scientists to identify species, this cannot be submitted to our Heritage Trust database until species are verified. We hope to follow up with volunteers to confirm species either through checking out an Echometer Touch bat call recording device to them, or through pictures they opportunistically take of the bats themselves.

Between 2017 and 2020, a total of 830 bat records were entered into our Heritage Trust database. Working with NABat, we submitted all our hibernacula and maternity colony bat data to date through the NABat online portal by June of 2019. Across South Carolina overall, we now have a total of 1,248 bat location records in our Heritage Trust database (Figure 2). These records include hibernacula, maternity colony, and netting data. Thus, some points are for single bats while others are for colonies whose information is updated every few years after each new survey. We look forward to using Survey123 for summary analyses of entered data in the future. By compiling data from around the state into our Heritage Trust database, it will be possible to observe trends more easily for species occurrence and population changes, as well as reproductive status and other morphological differences within each species across the state.

Significant deviations:

We originally proposed the use of Microsoft Access to record and store bat data. However, with the increasing access and utility of ArcGIS software, Survey123 apps, and online data storage, we decided it would be more pertinent to use ArcGIS online for data analysis and data sharing into the future.

Objective: Determine the summer roosting requirements of Northern Yellow Bats (*Lasiurus intermedius*), Tri-colored Bats (*Perimyotis subflavus*), and Northern Long-eared Bats (*Myotis septentrionalis*) at the structure (e.g. tree), stand, and landscape scales.

Accomplishments:

For complete results, see Kyle Shute's thesis "Habitat Relationships of Bat Species of Conservation Concern in Coastal South Carolina" in Appendix C.

To understand summer roost selection, we radio-tracked six Northern Yellow Bats (Table 2), seven PESU (Table 3), and two MYSE (Table 4) to roost trees May-August 2018 and 2019. We characterized used roost trees and associated available trees and used discrete choice models to analyze our data. Although we did not capture enough MYSE for resource selection analysis, we determined that one MYSE used bark roosts in slash pine (*Pinus taeda*) and one used a basal cavity in water tupelo (*Nyssa aquatica*) consistent with what others have documented (Confortin and Brown 2018; Kindel 2019). PESU and Northern Yellow Bats switched roosts frequently (every 1.3 days) and used 3.8 and 4.5 trees/bat over the tracking period (approximately 5-9 days), respectively. PESU roosted in foliage and Spanish moss (*Tillandsia usneoides*) in hardwood trees consistent with other studies (Menzel et al. 1999,

Veilleux et al. 2003). They avoided pine trees and selected trees with high densities of Spanish moss (Ch 1. Figure 2). Northern yellow bats roosted in dead palm fronds in cabbage palm trees (*Sabal palmetto*) or Spanish moss in hardwood trees consistent with findings of Castleberry et al. 2020. They selected cabbage palm trees and trees with high densities of Spanish moss or dead palm fronds (Ch 1. Figure 2). Our results suggest that conservation of maritime and bottomland forests with trees that have high densities of roost structures would benefit all three species and that further information, particularly about maternity colonies, is required to further inform managers.

Significant deviations: Given low capture rates of our primary target species in 2018, we added PESU as a target species in 2019. This species was recently proposed for listing under the Endangered Species Act, and significant declines have been observed in other areas of the range due to White-nose Syndrome (USFWS 2017). In 2018, PESU was one of our most captured species. Given the conservation concerns for this species and the apparent population size in the Coastal Plain of South Carolina, we determined that it should be included in our study.

Objective: Determine the characteristics of foraging areas (e.g. habitat type, age, structure, and landscape context) used by Northern Yellow Bats, Tri-colored Bats, and Northern Long-eared Bats in the Lower Coastal Plain of South Carolina during summer and winter.

Accomplishments:

For complete results, see Kyle Shute's thesis "Habitat Relationships of Bat Species of Conservation Concern in Coastal South Carolina" in Appendix C.

During summer and winter of 2018 and 2019, we surveyed 125 sites across our 3 study areas (Palmetto Bluff, Victoria Bluff, and Pinckney Island) for 4 nights (summer) and 5-10 nights (winter) using acoustic detectors. We stratified the areas into 5 habitat categories: Upland Forest, Bottomland Forest, Fields, Ponds, and Salt Marsh. We characterized forest structure and measured landscape covariates at each site and used occupancy modeling to understand seasonal habitat use in both summer and winter of Northern Yellow Bats, PESU, and *Myotis* bats. We grouped MYSE and Southeastern *Myotis* into *Myotis* spp. because of similarity in their call structure which makes it difficult to differentiate the species. *Myotis* spp. used sites that were closer to hardwood stands and freshwater year-round, and sites closer to pine stands during winter. During summer, PESU were present at most sites (85%) and use was not dependent on any characteristics we measured. However, during winter they used bottomland forests, fields, and ponds more than salt marsh and upland forests. During summer, Northern Yellow Bats used sites close to freshwater and salt marsh, and used fields, ponds, and salt marsh more than bottomland and upland forests. During winter, they continued to use sites close to salt marsh and freshwater, but used bottomland forests, fields, and ponds more than upland forest and salt marsh. Our results highlight the importance of specific forest stands and features like freshwater, salt marsh, ponds, and bottomland forests. These results also highlight that changes in habitat use occur between seasons and that failure to account for different ecological needs throughout the year may limit our understanding of important habitat features.

Significant deviations: Given high capture numbers in 2018 and the recent proposal of PESU to be added to the Endangered Species list, we added this species as one of interest to study foraging and nocturnal habitat use.

Literature Cited:

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Estimated Federal Cost: \$210,235

Recommendations: Close the grant. Continued research and monitoring to better understand MYSE in South Carolina, specifically in the southern coastal plains within its range, is greatly needed for additional information on location, habitat use and population dynamics for this Federally Threatened species.

Submitted by Jennifer Kindel, SCDNR on 4/13/2021

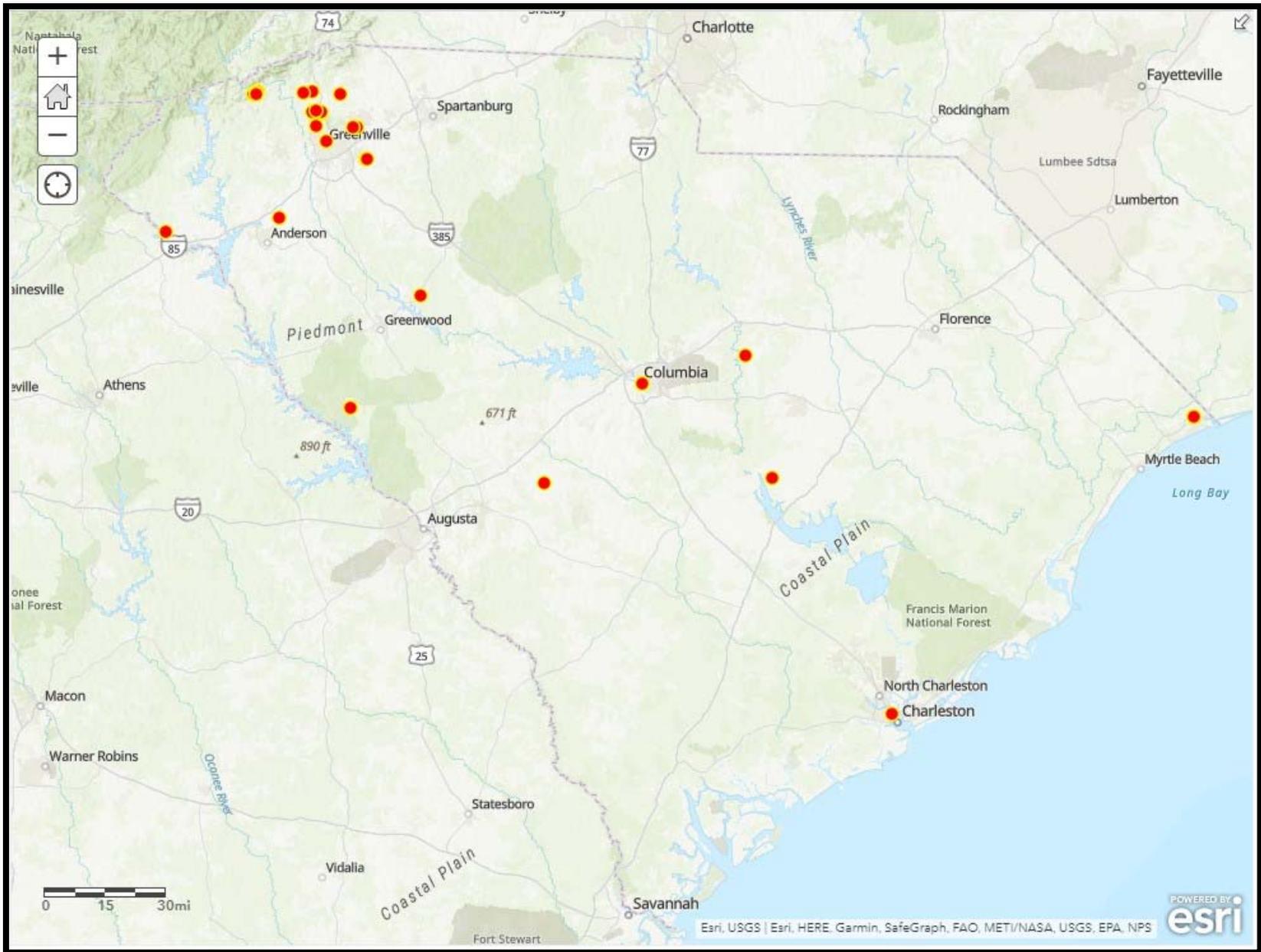


Figure 1: SC Bat Watch! survey locations from 2018- 2020.

Table 2. Northern Yellow Bat (individuals labeled as LAIN01-LAIN06) roost trees used in summer 2018 and 2019 in Bluffton, SC.

Bat #	Band Prefix	Band	1 st Date Tracked	Tree #	<i>Spp.</i>	Lat	Long	# of Roost Nights in Tree
LAIN-01	SBDN	C0098	6/20/2018	T-01	<i>Sabal palmetto</i>	32.1470666	-80.9227236	1
LAIN-01	SBDN	C0098	6/21/2018	T-02	<i>Sabal palmetto</i>	32.1462736	-80.9237519	1
LAIN-01	SBDN	C0098	6/22/2018	T-03	<i>Sabal palmetto</i>	32.1469479	-80.9239441	6
LAIN-01	SBDN	C0098	6/26/2018	T-04	<i>Sabal palmetto</i>	32.1401468	-80.9297862	1
LAIN-01	SBDN	C0098	6/27/2018	T-05	<i>Sabal palmetto</i>	32.1476033	-80.9224557	1
LAIN-01	SBDN	C0098	6/28/2018	T-06	<i>Sabal palmetto</i>	32.1471380	-80.9223818	1
LAIN-01	SBDN	C0098	7/1/2018	T-07	<i>Sabal palmetto</i>	32.1405485	-80.9284034	1
LAIN-02	SBDN	C0130	5/19/2019	T-01	<i>Sabal palmetto</i>	32.1801928	-80.8965696	1
LAIN-02	SBDN	C0130	5/20/2019	T-02	<i>Sabal palmetto</i>	32.1805112	-80.8960872	1
LAIN-02	SBDN	C0130	5/21/2019	T-03	<i>Sabal palmetto</i>	32.1799243	-80.8962748	1
LAIN-02	SBDN	C0130	5/22/2019	T-04	<i>Sabal palmetto</i>	32.1799688	-80.8956184	1
LAIN-02	SBDN	C0130	5/23/2019	T-05	<i>Sabal palmetto</i>	32.1802809	-80.8965944	1
LAIN-03	SBDN	C0089	5/24/2019	T-01	<i>Nyssa aquatica</i>	32.1736423	-80.9048530	1
LAIN-04	SBDN	C0125	6/20/2019	T-01	<i>Quercus laurifolia</i>	32.1739453	-80.9011629	1
LAIN-04	SBDN	C0125	6/21/2019	T-02	<i>Quercus virginiana</i>	32.1718662	-80.9002545	1
LAIN-04	SBDN	C0125	6/22/2019	T-03	<i>Quercus laurifolia</i>	32.1739966	-80.9000210	1
LAIN-04	SBDN	C0125	6/23/2019	T-04	<i>Nyssa aquatica</i>	32.1717642	-80.8997033	1
LAIN-04	SBDN	C0125	6/25/2019	T-05	<i>Nyssa aquatica</i>	32.1748040	-80.9020881	1
LAIN-04	SBDN	C0125	6/26/2019	T-06	<i>Quercus virginiana</i>	32.1719844	-80.9004321	1
LAIN-04	SBDN	C0125	6/27/2019	T-07	<i>Quercus nigra</i>	32.1729293	-80.8995096	2
LAIN-04	SBDN	C0125	6/29/2019	T-08	<i>Quercus virginiana</i>	32.1749838	-80.9021262	1
LAIN-04	SBDN	C0125	6/30/2019	T-09	<i>Quercus virginiana</i>	32.1752207	-80.8998486	3
LAIN-05	SBDN	C0126	6/27/2019	T-01	<i>Quercus virginiana</i>	32.1455802	-80.9300175	1
LAIN-06	SBDN	C0129	7/9/2019	T-01	<i>Quercus nigra</i>	32.2638265	-80.8232094	1
LAIN-06	SBDN	C0129	7/10/2019	T-02	<i>Quercus virginiana</i>	32.2668646	-80.8271235	1
LAIN-06	SBDN	C0129	7/11/2019	T-03	<i>Quercus laurifolia</i>	32.2648304	-80.8232922	1
LAIN-06	SBDN	C0129	7/12/2019	T-04	<i>Quercus chapmanii</i>	32.2671014	-80.8236898	3

Table 3. Tri-colored Bat (individuals labeled as PESU01-PESU07) roost trees used in summer 2019 in Bluffton, SC.

Bat #	Band Prefix	Band	1 st Date Tracked	Tree #	Spp.	Lat	Long	# Roost Nights in Tree
PESU-01	USFS/SRS	SR0477	6/15/2019	T-01	<i>Liquidambar styraciflua</i>	32.19178002	-80.91140334	1
PESU-01	USFS/SRS	SR0477	6/16/2019	T-02	<i>Quercus nigra</i>	32.19108361	-80.91323231	1
PESU-01	USFS/SRS	SR0477	6/17/2019	T-03	<i>Liquidambar styraciflua</i>	32.19249135	-80.91058597	1
PESU-01	USFS/SRS	SR0477	6/18/2019	T-04	<i>Pinus taeda</i>	32.19184085	-80.91145696	1
PESU-01	USFS/SRS	SR0477	6/19/2019	T-05	<i>Quercus nigra</i>	32.19140183	-80.91218093	1
PESU-01	USFS/SRS	SR0477	6/20/2019	T-06	<i>Quercus laurifolia</i>	32.19160067	-80.91238952	1
PESU-01	USFS/SRS	SR0477	6/21/2019	T-07	<i>Liquidambar styraciflua</i>	32.19113937	-80.91074914	2
PESU-01	USFS/SRS	SR0477	6/23/2019	T-08	<i>Quercus virginiana</i>	32.19296635	-80.91014910	1
PESU-02	USFS/SRS	SR0476	7/4/2019	T-01	<i>Magnolia virginianus</i>	32.19252043	-80.93016586	1
PESU-03	USFS/SRS	SR0461	7/5/2019	T-01	<i>Quercus virginiana</i>	32.17527971	-80.90003655	2
PESU-03	USFS/SRS	SR0461	7/7/2019	T-02	<i>Liquidambar styraciflua</i>	32.17316414	-80.90062162	1
PESU-03	USFS/SRS	SR0461	7/8/2019	T-03	<i>Acer rubrum</i>	32.17417842	-80.90019551	1
PESU-03	USFS/SRS	SR0461	7/9/2019	T-04	<i>Magnolia grandifolia</i>	32.17383464	-80.90066999	1
PESU-03	USFS/SRS	SR0461	7/10/2019	T-05	<i>Quercus virginiana</i>	32.17350000	-80.90070000	1
PESU-04	USFS/SRS	SR0475	7/10/2019	T-01	<i>Liquidambar styraciflua</i>	32.24560197	-80.76313474	1
PESU-04	USFS/SRS	SR0475	7/12/2019	T-02	<i>Liquidambar styraciflua</i>	32.24653034	-80.76214931	1
PESU-05	USFS/SRS	SR0462	7/10/2019	T-01	<i>Quercus virginiana</i>	32.24082994	-80.75356161	2
PESU-05	USFS/SRS	SR0462	7/12/2019	T-02	<i>Quercus virginiana</i>	32.24151056	-80.75482098	1
PESU-05	USFS/SRS	SR0462	7/13/2019	T-03	<i>Quercus virginiana</i>	32.24142158	-80.75519308	2
PESU-05	USFS/SRS	SR0462	7/15/2019	T-04	<i>Quercus virginiana</i>	32.24084892	-80.75429934	1
PESU-06	USFS/SRS	SR0463	7/19/2019	T-01	<i>Liquidambar styraciflua</i>	32.19514789	-80.90710106	3
PESU-06	USFS/SRS	SR0464	7/21/2019	T-02	<i>Quercus laurifolia</i>	32.19509406	-80.9071048	1
PESU-07	USFS/SRS	SR0464	7/20/2019	T-01	<i>Celtis laevigata</i>	32.18947536	-80.87999995	1
PESU-07	USFS/SRS	SR0465	7/21/2019	T-02	<i>Celtis laevigata</i>	32.18940697	-80.87970844	1
PESU-07	USFS/SRS	SR0466	7/22/2019	T-03	<i>Celtis laevigata</i>	32.18957668	-80.87978020	2

Table 4. Northern Long-eared Bat (individuals labeled as MYSE01-MYSE02) roost trees used in summer 2018 and 2019 in Bluffton, SC.

Bat #	Band Prefix	Band	1 st Date Tracked	Tree #	Spp.	Lat	Long	# Roost Night in Tree
MYSE-01	USFS/SRS	4274	7/23/2018	T-01	<i>Pinus elliottii</i>	32.18910776	-80.90136804	5
MYSE-01	USFS/SRS	4274	7/26/2018	T-02	<i>Pinus elliottii</i>	32.18862337	-80.90205615	1
MYSE-01	USFS/SRS	4274	5/6/2019	T-03	<i>Pinus elliottii</i>	32.17971591	-80.91286568	1
MYSE-01	USFS/SRS	4274	5/7/2019	T-04	<i>Pinus elliottii</i>	32.18067426	-80.91090398	1
MYSE-01	USFS/SRS	4274	5/8/2019	T-05	<i>Pinus elliottii</i>	32.17627000	-80.91328000	5
MYSE-02	DB	1254	5/25/2019	T-01	<i>Nyssa aquatica</i>	32.16070302	-80.92036250	6
MYSE-02	DB	1254	5/26/2019	T-02	<i>Nyssa aquatica</i>	32.16011202	-80.92048244	1

See attached:

Appendix A: Northern Long-eared Bat Project at Santee Coastal Reserve Wildlife Management Area and The Nature Conservancy Washo Reserve. 2018 – 2019 General Report.

Appendix B: Wildlife Control Operator letter sent on September 10, 2020.

Appendix C: Habitat Relationships of Bat Species of Conservation Concern in Coastal South Carolina, master's thesis by Kyle Shute

Northern Long-eared Bat Project

At Santee Coastal Reserve Wildlife Management Area

and The Nature Conservancy Washo Reserve

2018 – 2019 General Report



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Summary

A total of eight Northern long-eared bats (*Myotis septentrionalis*, or MYSE) have been captured during the summers of 2018 and 2019 at Santee Coastal Reserve Wildlife Management Area (WMA) and Washo Reserve in the South Carolina coastal plain. These include 2 subadults (1 male, 1 female), 3 adult males, and 3 pregnant females. The subadults, 1 adult male, and 2 pregnant females were fitted with radio transmitters and tracked to day roost sites. A sweetgum (*Liquidambar styraciflua*) cavity within 300 feet of the capture location was used by the adult male for at least 5 days. All females roosted under bark of live, mature longleaf pine (*Pinus palustris*) within 150 feet of a road, in uniform aged stands approx. 85 years old undergoing frequent fire (1 to 5 years) and managed for local populations of endangered red-cockaded woodpeckers (*Leuconotopicus borealis*). Average female roost tree (n = 10) characteristics were 30% canopy closure, 14-inch DBH, 30% exfoliating bark, and approximately 58 feet tall. All females were found to switch roosts daily, and distances between the previous roost varied between 5 and 1,200 feet. Only one roost tree was used twice. Females generally roosted alone, and no maternity colonies were found. Capture locations for females were about 1 mile away from their day roosts, and capture site habitat varied greatly from that of day roosts. Females were tracked to longleaf pine roosts from captures sites in either a mixed hardwood pond area (subadult female) or closed canopy near-maritime forest (both pregnant females). We suspect capture sites were primarily foraging areas. We estimate the pup season for this population to be between late April and early May, approximately one month earlier than that outlined in the current 4(d) rule. Swabbing for the fungus that causes White-nose Syndrome tested was conducted both years, and results were negative for the fungus.

Introduction

The South Carolina Department of Natural Resources, through funding from State Wildlife Grants and the US Fish and Wildlife Service White-nose Syndrome Grants to States, continues to seek location and roost information for the federally threatened Northern long-eared bat on the South Carolina coastal plain. The Northern long-eared bat is a federally threatened species due to 90-100% mortality and dramatic population declines from White-nose Syndrome (WNS). This species was only recently discovered on the SC coastal plain in 2016, far from the southern end of its range in the Upstate. Northern long-eared bats were first discovered on the coast in November 2016 at [Palmetto Bluff Conservancy in Beaufort County](#) with one adult male and one juvenile female. At Francis Marion National Forest in 2017, they were found [breeding in Charleston and Berkeley counties](#). By 2018, a total of 20 individuals had been captured at Francis Marion National Forest and included all sex and age classes except pregnant females. At Palmetto Bluff Conservancy in 2018, Clemson graduate student Kyle Shute captured one adult male. This year, the same male was recaptured, along with two additional adult males, providing an unprecedented opportunity to collect multiyear coastal summer roost information with the same individual. Including SCDNR's contribution outlined in this report, a total of 33 Northern long-eared bats have been netted in the SC coastal plain to date, thanks to the people and organizations working to understand this species' distribution and habitat use.

However, much remains to be understood about these populations, as evidenced by the fact that it was only this year that [pregnant MYSE](#) were captured for the first time on the South Carolina

coast. This discovery by SCDNR at Santee Coastal Reserve WMA and Washo Reserve is what is described in this report.

Santee Coastal Reserve WMA is 24,000 acres encompassing the freshwater cypress swamp of The Nature Conservancy's 1,040-acre Washo Reserve, diverse uplands including mature longleaf pine stands, Carolina Bays, and mixed hardwoods; and freshwater, brackish and tidal wetlands and agricultural fields. Within and amongst these unique habitat types, we captured MYSE near freshwater marsh in closed canopy near-maritime forests with a loblolly pine-hardwood component and tracked them to their roosts in longleaf pines.

Methods

To capture bats, Avinet Polyester 38mm mesh bat nets set single, double, or triple high using Bat Conservation and Management Triple High Mist Net Pole System were used. Net locations were generally placed underneath closed forest canopy and across fly-way corridors such as road beds, trails, or streams. Bat calls were opportunistically recorded using two Anabat Express devices. This acoustic data was analyzed using a BCID program and helped determine best net placement for areas with high *Myotis* calls.

When bats of any species were captured, we recorded species, sex, reproductive stage, and morphometric data into a Survey123 app, which was promptly submitted into our online Heritage Trust database. Aluminum bands affixed to the forearm were mainly used on MYSE. When any Northern long-eared bat was captured, a Holohil Systems LB-2X or BD-2X radio-tag less than 5% of the body weight of the bat was affixed to a trimmed area between the scapulae using Perma-Type Surgical Cement.

Using a TR-2 Telonics receiver and folding 3-element Yagi antennae, we tracked radio-tagged bats daily for the life of the transmitter or until the unit dropped from the bat. For each identified roost, we recorded details such as tree species, diameter at breast height (dbh; inches), height of tree (feet), approx. height of roost (feet), canopy closure at roost (%), exfoliating bark on bole (%), cavities present (y/n) and decay state (1-9). We performed emergence counts at day-roosts used by radio-tracked bats to estimate colony size.

Additional assistance from staff, interns, and volunteers was provided, though anyone handling bats were required to have up-to-date pre-exposure rabies shots or titers and the necessary permits to handle MYSE.

Results

Overall

A total of 8 MYSE were captured: 2 subadults (1 male, 1 female), 3 adult males, and 3 pregnant females. The subadults, 1 adult male, and 2 pregnant females were fitted with radio transmitters and tracked to day roost sites. A total of 8 capture locations, 16 day roost sites, and 2 locations where the transmitter had been dropped were recorded (Table 1, Figures 1 - 3). Of the day roost sites, pregnant females made up half (8), the subadult female was found at 5, the subadult male at 2 (estimated locations only) and the adult male found at 1 roost.

Table 1: Northern long-eared bat locations, summers of 2018 and 2019. S = subadult, A = adult, NR = Non-reproductive, P = pregnant, F = female, M = male. Locations in light red are approximate.

Date	Type	Age	Repro	Sex	Band	Frequency	Latitude	Longitude
6/5/2018	Capture	S	NR	F	A195	151.782	33.145850	-79.405410
6/6/2018	Capture	S	NR	M	None	151.741	33.145850	-79.405410
6/6/2018	Capture	A	NR	M	None	None	33.145150	-79.405260
6/6/2018	Roost	S	NR	F	A195	151.782	33.148670	-79.391910
6/7/2018	Roost	S	NR	F	A195	151.782	33.148230	-79.393830
6/8/2018	Roost	S	NR	M	None	151.741	33.148097	-79.406004
6/12/2018	Roost	S	NR	F	A195	151.782	33.148193	-79.393417
6/14/2018	Roost	S	NR	F	A195	151.782	33.148330	-79.393300
6/15/2018	Roost	S	NR	F	A195	151.782	33.148310	-79.393300
6/15/2018	Roost	S	NR	M	None	151.741	33.153820	-79.406470
4/17/2019	Capture	A	NR	M	A201	151.420	33.143440	-79.404708
4/18/2019	Roost	A	NR	M	A201	151.420	33.143990	-79.405080
4/26/2019	Dropped	A	NR	M	A201	151.420	33.152030	-79.366380
4/29/2019	Capture	A	P	F	A208	151.820	33.155087	-79.382307
4/29/2019	Capture	A	P	F	A211	151.300	33.155087	-79.382307
4/30/2019	Capture	A	P	F	A213	None	33.154904	-79.379782
4/30/2019	Roost	A	P	F	A208	151.820	33.150200	-79.390010
4/30/2019	Roost	A	P	F	A211	151.300	33.147900	-79.394490
5/1/2019	Roost	A	P	F	A208	151.820	33.150430	-79.389990
5/1/2019	Roost	A	P	F	A211	151.300	33.147480	-79.394390
5/2/2019	Capture	A	NR	M	A216	None	33.155079	-79.378861
5/2/2019	Roost	A	P	F	A208	151.820	33.153070	-79.390410
5/2/2019	Roost	A	P	F	A211	151.300	33.147900	-79.394490
5/3/2019	Roost	A	P	F	A208	151.820	33.153080	-79.390340
5/3/2019	Roost	A	P	F	A211	151.300	33.148190	-79.393034
5/7/2019	Dropped	A	P	F	A208	151.820	33.156473	-79.383357

The subadult male locations (light red text in Table 1) were approximate due to receiver difficulties during a rainstorm when tracking to the first location, and inaccessibility of the marsh with the second location. No roost information for these locations were collected. In addition, characteristics from 2 identified roosts of the subadult female from 6/14 - 6/15/2018 were not recorded as only the roost location was collected by a volunteer. However, these longleaf pine roosts were all in a uniform age stand within approximately 300 feet of the other 3 longleaf pine roosts with characteristics documented for the same subadult female.

The adult male utilized a cavity roost for at least 5 days before the transmitter was dropped in bottomland hardwood swamp 2.75 miles away. The cavity tree was sweetgum, had 75% canopy

closure, 21.3-inch DBH, 10% exfoliating bark, was approximately 70 feet tall, had a basal cavity opening of 6.5 inches wide by 4.5 inches tall with a cavity height of at least 3 feet. The cavity tree was 275 feet from the capture location on Sandpit Road near a pond within longleaf pine savannah.

All females roosted under bark of live, mature longleaf pine within 150 feet of a road (Figures 4 & 5), in 85-year-old stands undergoing frequent fire (approximately 2-5 years). Average female roost tree characteristics ($n = 10$) were 30% canopy closure, 14-inch DBH, 30% exfoliating bark, and were approximately 58 feet tall. The general understory of all longleaf pine roosts included ferns, poison oak, blackberries, and other low growing scrub.

All females were found to switch roosts daily, and distances between the previous roost varied between 5 and 1,200 feet. Only one roost tree was used twice, by a pregnant female. Emergence counts showed that all females roosted alone, with one exception of a pregnant female seen roosting with one other bat in the same tree used twice. No maternity colonies were found.

Capture locations for females were about 1 mile away from their day roosts, and capture site habitat varied greatly from that of day roosts. Females were tracked to longleaf pine roosts from captures sites in either a mixed hardwood pond area (subadult female) or closed canopy near-maritime forest (both pregnant females). We suspect capture sites were primarily foraging areas as the receiver was periodically turned on during netting, and strong signals from the subadult female and pregnant females could be heard in the netting locations we had captured them previous.

We estimate the pup season for this population to be between late April and early May, approximately one month earlier than the June 1 – July 31 pup season outlined in the current 4(d) rule. We initially captured volant (flying) juvenile Northern long-eared bats in early June 2018. Because it takes at least three weeks for the young to begin to fly, those individuals were born no later than mid-May. Finding heavily pregnant females in late April 2019 suggests pups were likely born in early May.

Swabbing for the fungus that causes White-nose Syndrome, *Pseudogymnoascus destructans* or *Pd*, was conducted in cooperation with the National Wildlife Health Center both years. In 2018, swabs for 13 tri-colored bats, 9 southeastern myotis, 1 evening bat, 1 northern long-eared bat, and 1 environmental were taken. In 2019, swabs for 12 big brown bats, 5 northern long-eared bats, 5 southeastern bats, 2 tri-colored bats and 1 environmental were taken. In addition, 15 guano pellets were collected. In 2018 and 2019, all combined wing/muzzle swabs, environmental sample, and guano pellets collected tested negative for *Pd*, the causative agent of white-nose syndrome (WNS), by real-time PCR. Note the lack of a positive result by PCR does not definitively indicate the absence of the organism. PCR may not detect the organism if it is at very low abundance in the sample.

Figure 1: Overview of Northern long-eared bat locations at Santee Coastal Reserve WMA and Washo Reserve from 2018-2019.

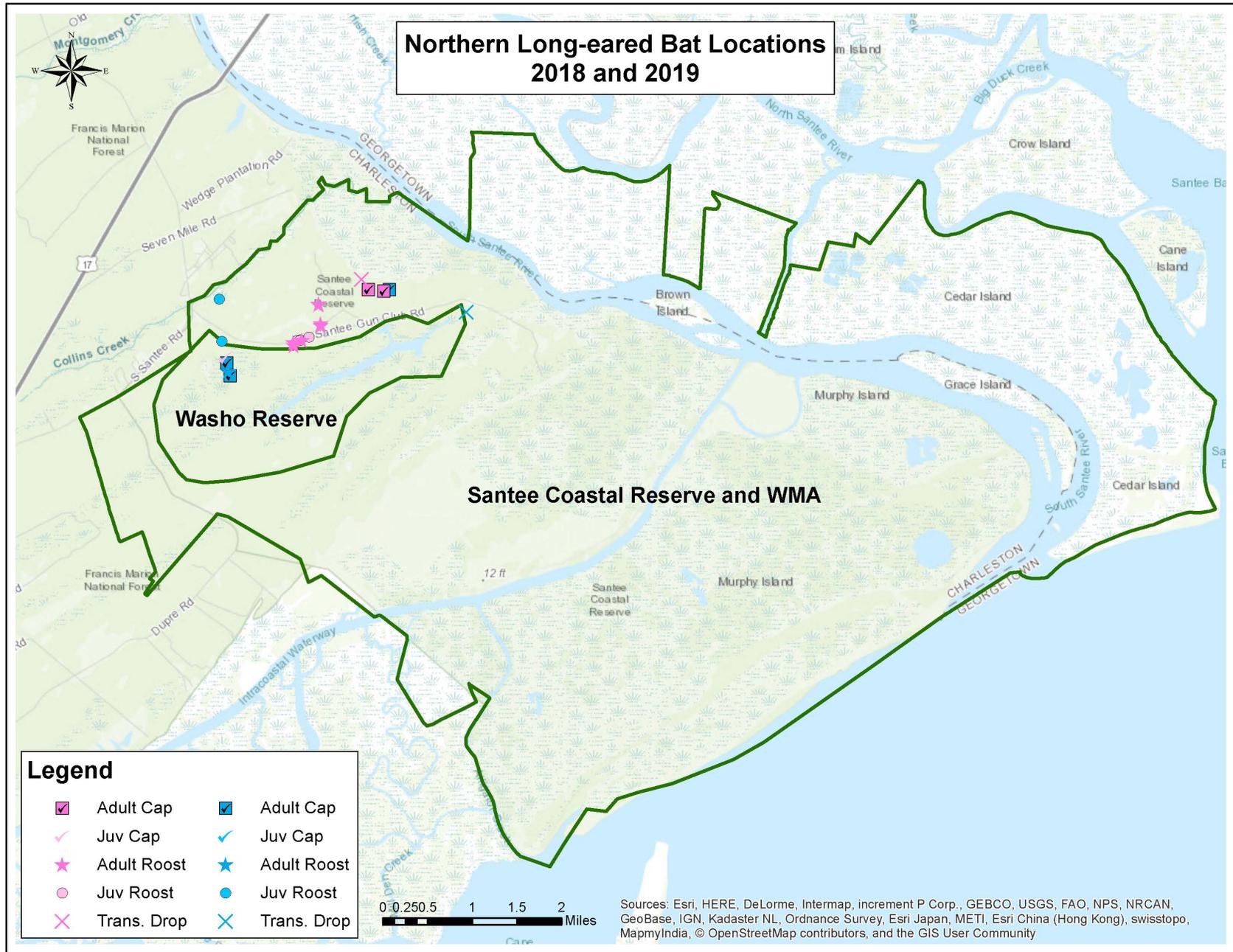


Figure 2: Topo of Northern long-eared bat locations at Santee Coastal Reserve WMA and Washo Reserve from 2018-2019.

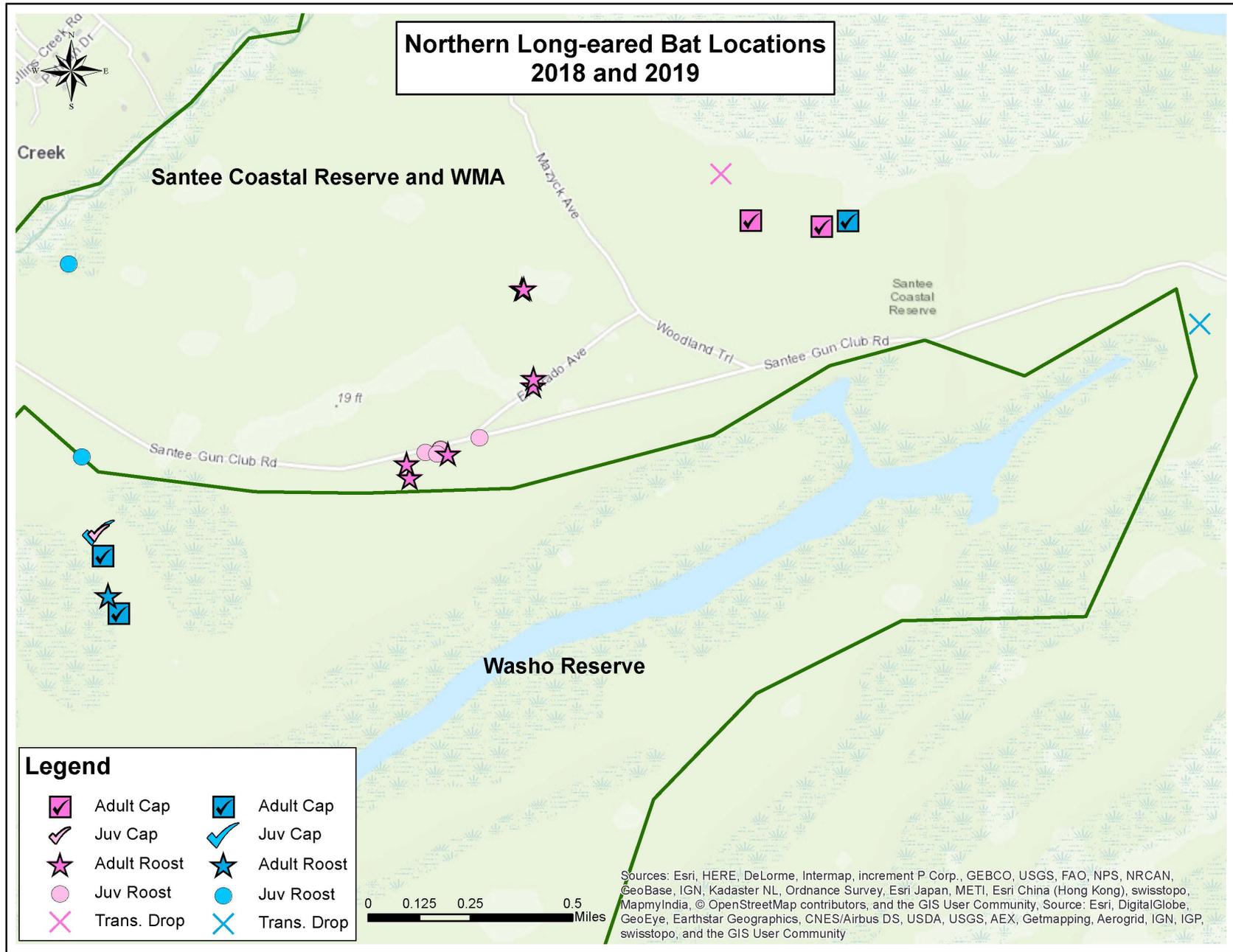


Figure 3: Imagery of Northern long-eared bat locations at Santee Coastal Reserve WMA and Washo Reserve from 2018-2019.

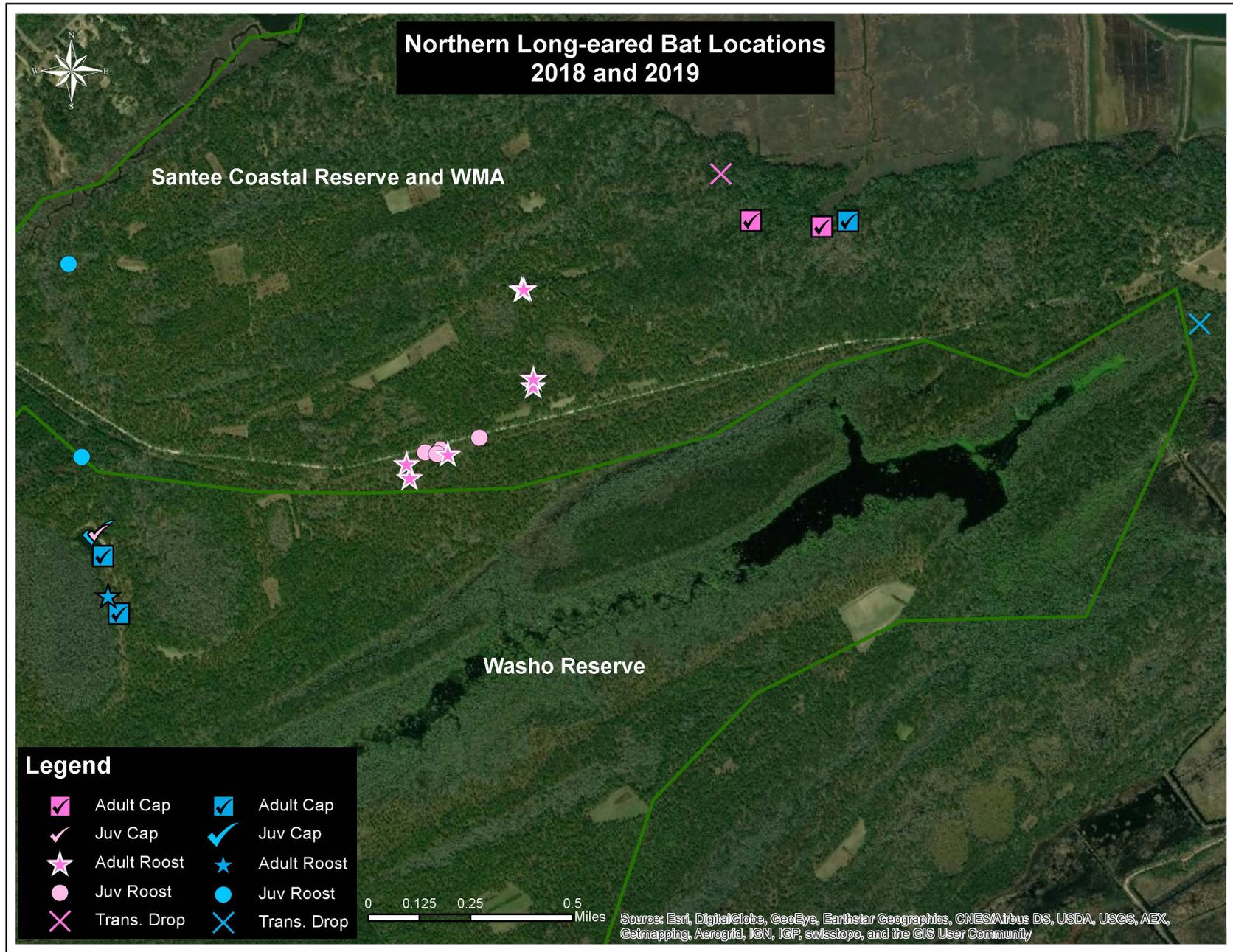


Figure 4: Imagery of female Northern long-eared bat locations at Santee Coastal Reserve WMA and Washo Reserve from 2018-2019.

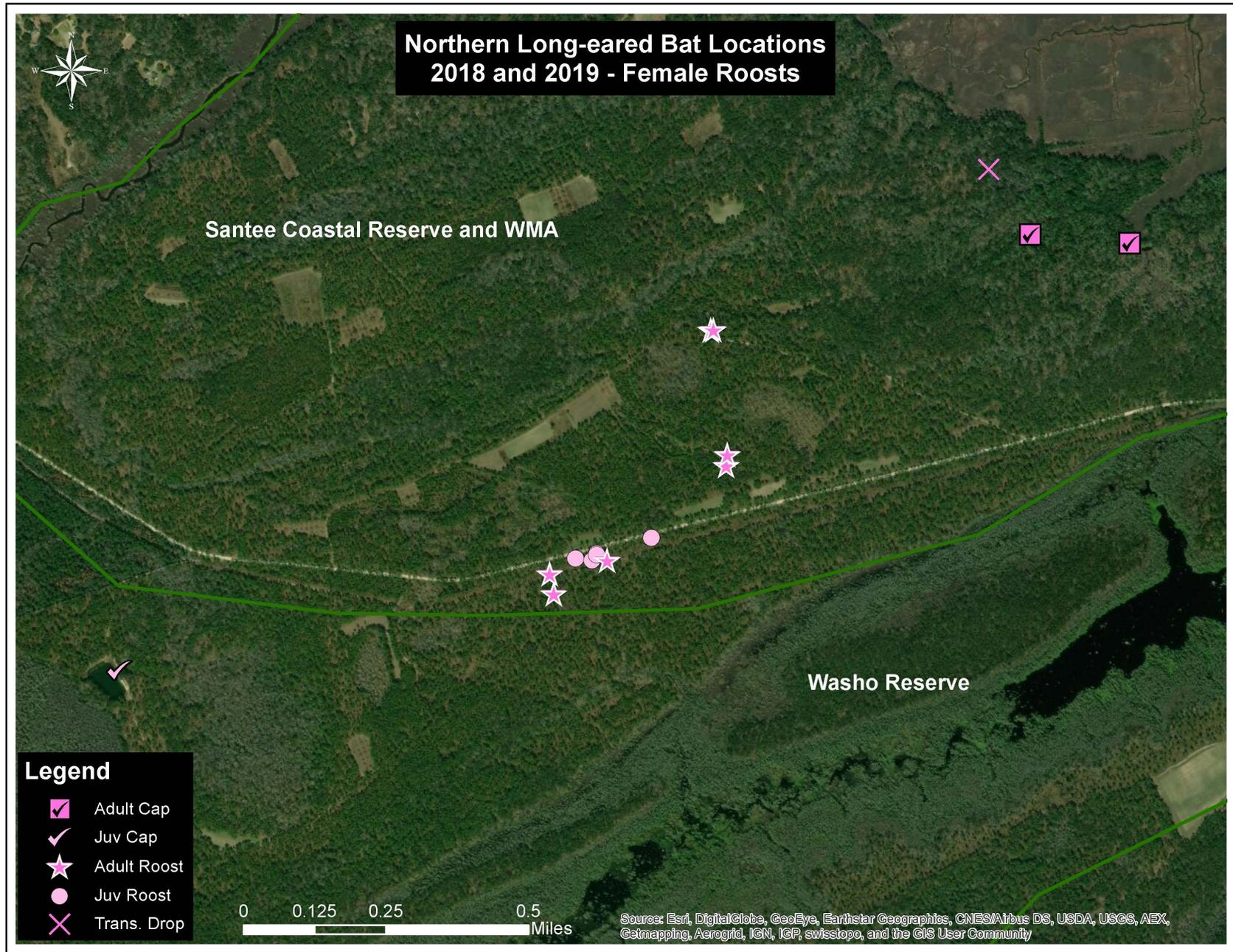
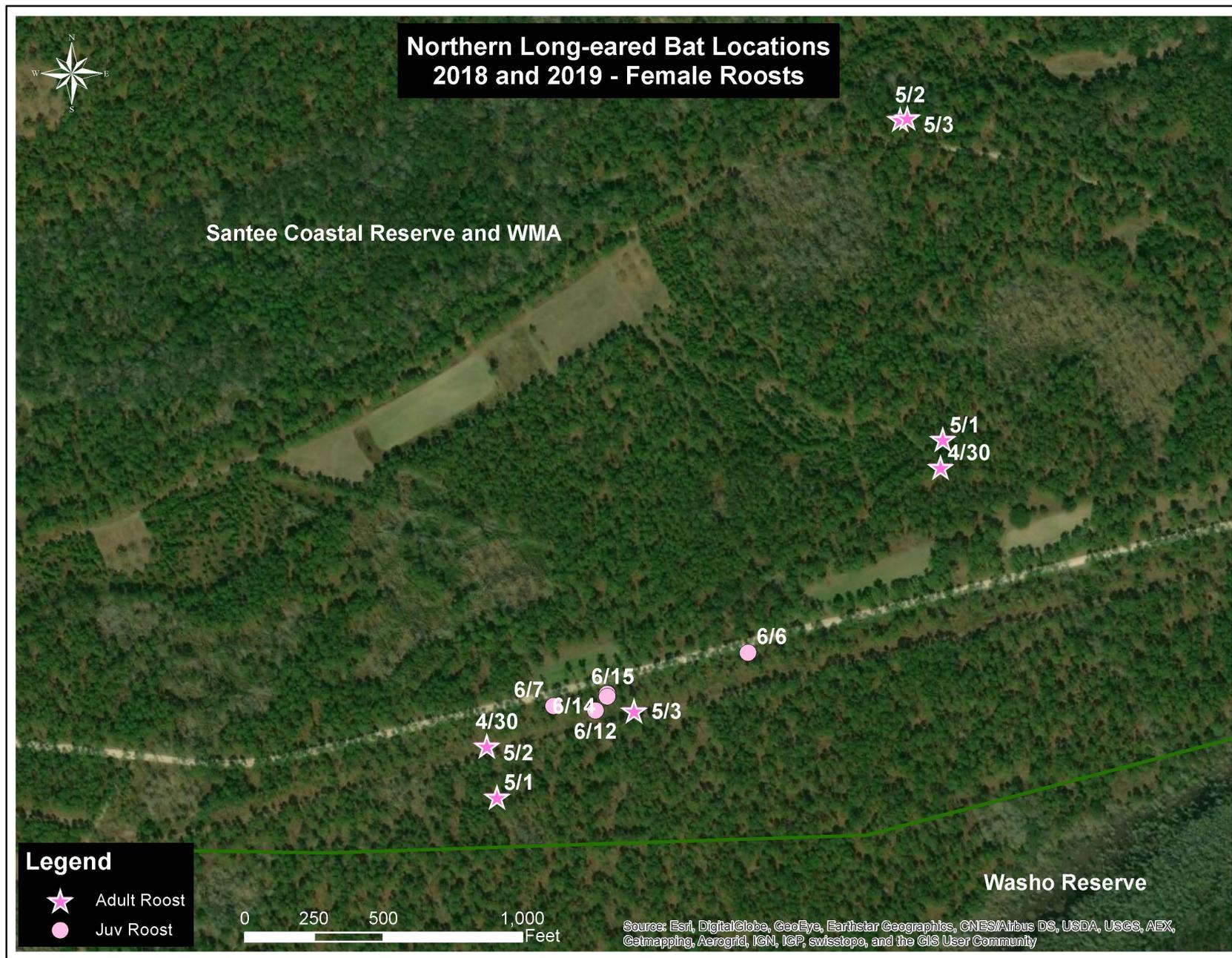


Figure 5: Imagery of female Northern long-eared bat roosts at Santee Coastal Reserve WMA and Washo Reserve from 2018-2019.



By Individual

Subadult male, Frequency 151.741. Maps in Appendix A

Date	Type	Age	Repro	Sex	Band	Frequency	Latitude	Longitude
6/6/2018	Capture	S	NR	M	None	151.741	33.145850	-79.405410
6/8/2018	Roost	S	NR	M	None	151.741	33.148097	-79.406004
6/15/2018	Roost	S	NR	M	None	151.741	33.153820	-79.406470

We were only able to locate the sub-adult male MYSE on two occasions, 6/8 and 6/15/18. On 6/8 he was approximately 840 feet north of the capture location. The exact tree was not determined due to a rain storm, but he was likely in a long leaf pine near the edge of a small creek around 33.148097, -79.406004. On 6/15 he was located near Collins Creek approximately 3000 feet north of the capture location. We were unable to determine the exact tree he was roosting in due to swampy terrain, but it was near the point 33.15382, -79.40647.

Adult male, Frequency 151.420. Maps in Appendix B.

Date	Type	Age	Repro	Sex	Band	Frequency	Latitude	Longitude
4/17/2019	Capture	A	NR	M	A201	151.420	33.143440	-79.404708
4/18/2019	Roost	A	NR	M	A201	151.420	33.143990	-79.405080
4/26/2019	Dropped	A	NR	M	A201	151.420	33.152030	-79.366380

A single sweetgum roost with basal cavity was used from 4/18/, 4/20, 4/23, 4/24, and 4/25/19. The cavity tree species was sweetgum, it had 75% canopy closure, 21.3-inch DBH, 10% exfoliating bark, was approximately 70 feet tall, had a basal cavity opening of 6.5 inches wide by 4.5 inches tall, and a cavity height of at least 3 feet. Emergence count conducted on 4/22 showed one bat emerged from roost and left, but transmitter bat stayed until it was too dark to see. The cavity tree was 275 feet north-northwest of the capture location, which was on Sandpit Road near a Sandpit pond within longleaf pine savannah. The transmitter was found in the mud of bottomland swamp in Washo Reserve on 4/26, 2.75 miles east-northeast from the roost site.

Subadult female, Frequency 151.782. Maps in Appendix C

Date	Type	Age	Repro	Sex	Band	Frequency	Latitude	Longitude
6/5/2018	Capture	S	NR	F	A195	151.782	33.145850	-79.405410
6/6/2018	Roost	S	NR	F	A195	151.782	33.148670	-79.391910
6/7/2018	Roost	S	NR	F	A195	151.782	33.148230	-79.393830
6/12/2018	Roost	S	NR	F	A195	151.782	33.148193	-79.393417
6/14/2018	Roost	S	NR	F	A195	151.782	33.148330	-79.393300
6/15/2018	Roost	S	NR	F	A195	151.782	33.148310	-79.393300

Roosts, all under the bark of live longleaf pine, were located within 60 feet of a gravel or dirt road. All roosts were located 4,250 feet east-northeast of the capture location and within approximately 300 feet of each other in a uniform age stand of longleaf. Roost tree measurements were between 13 and 17 inches DBH, 20-25% canopy closure, 15-30% exfoliating bark and approximately 50 feet tall.

Pregnant female, Frequency 151.300. Maps in Appendix D

Date	Type	Age	Repro	Sex	Band	Frequency	Latitude	Longitude
4/29/2019	Capture	A	P	F	A211	151.300	33.155087	-79.382307
4/30/2019	Roost	A	P	F	A211	151.300	33.147900	-79.394490
5/1/2019	Roost	A	P	F	A211	151.300	33.147480	-79.394390
5/2/2019	Roost	A	P	F	A211	151.300	33.147900	-79.394490
5/3/2019	Roost	A	P	F	A211	151.300	33.148190	-79.393034

Roosts, all under the bark of live longleaf pine, were located within 150 feet of a gravel or dirt road. All roosts were approximately 1 mile southwest of the capture location and within approximately 550 feet of each other in a uniform age stand of longleaf. Roost tree measurements ranged between 14.7 and 15 inches DBH, 20-40% canopy closure, 25-30% exfoliating bark and approximately 65 feet tall.

Pregnant female, Frequency 151.820. Maps in Appendix E

Date	Type	Age	Repro	Sex	Band	Frequency	Latitude	Longitude
4/29/2019	Capture	A	P	F	A208	151.820	33.155087	-79.382307
4/30/2019	Roost	A	P	F	A208	151.820	33.150200	-79.390010
5/1/2019	Roost	A	P	F	A208	151.820	33.150430	-79.389990
5/2/2019	Roost	A	P	F	A208	151.820	33.153070	-79.390410
5/3/2019	Roost	A	P	F	A208	151.820	33.153080	-79.390340
5/7/2019	Dropped	A	P	F	A208	151.820	33.156473	-79.383357

Roosts, all under the bark of live longleaf pine, were located within 85 feet of a gravel or dirt road. Roosts on 4/30 and 5/1 were approximately 3,500 feet southwest of the capture location and 100 feet of each other in a uniform age stand of longleaf. Roosts on 5/2 and 5/3 were approximately 3,000 feet west-southwest of the capture location, 25 feet of each other in a uniform age stand of longleaf, and 1,200 feet north of the previous two roosts. Roost tree measurements ranged between 11.8 and 14.5 inches DBH, 20-60% canopy closure, 20-60% exfoliating bark and approximately 58 feet tall. The transmitter was found on 5/7 in the bark of a tree in closed canopy near-maritime forest 3,000 feet east-northeast from the previous roost site and 700 feet north-northwest of the capture location. We believe the bat pulled itself loose from the transmitter when the end of the transmitter antennae became stuck in the bark.

Discussion

These results show the first ever captures of pregnant Northern long-eared bats and characteristics of their roosts on the South Carolina Coastal Plain. Both pregnant females roosted under the bark of live, 85-year-old longleaf pine with low canopy closure and frequent fire. As can be expected, past roosting habitat of MYSE thought to only be in the mountains vary greatly from those in the coastal plain. Upstate roosts included mature mixed hardwood forest, mature Virginia pine stands, hemlock forest and mixed pine-hardwood less than 15 years old. Sadly, since WNS was first confirmed in SC in 2013, Northern long-eared bat records in the Upstate have become almost nonexistent despite similar survey efforts.

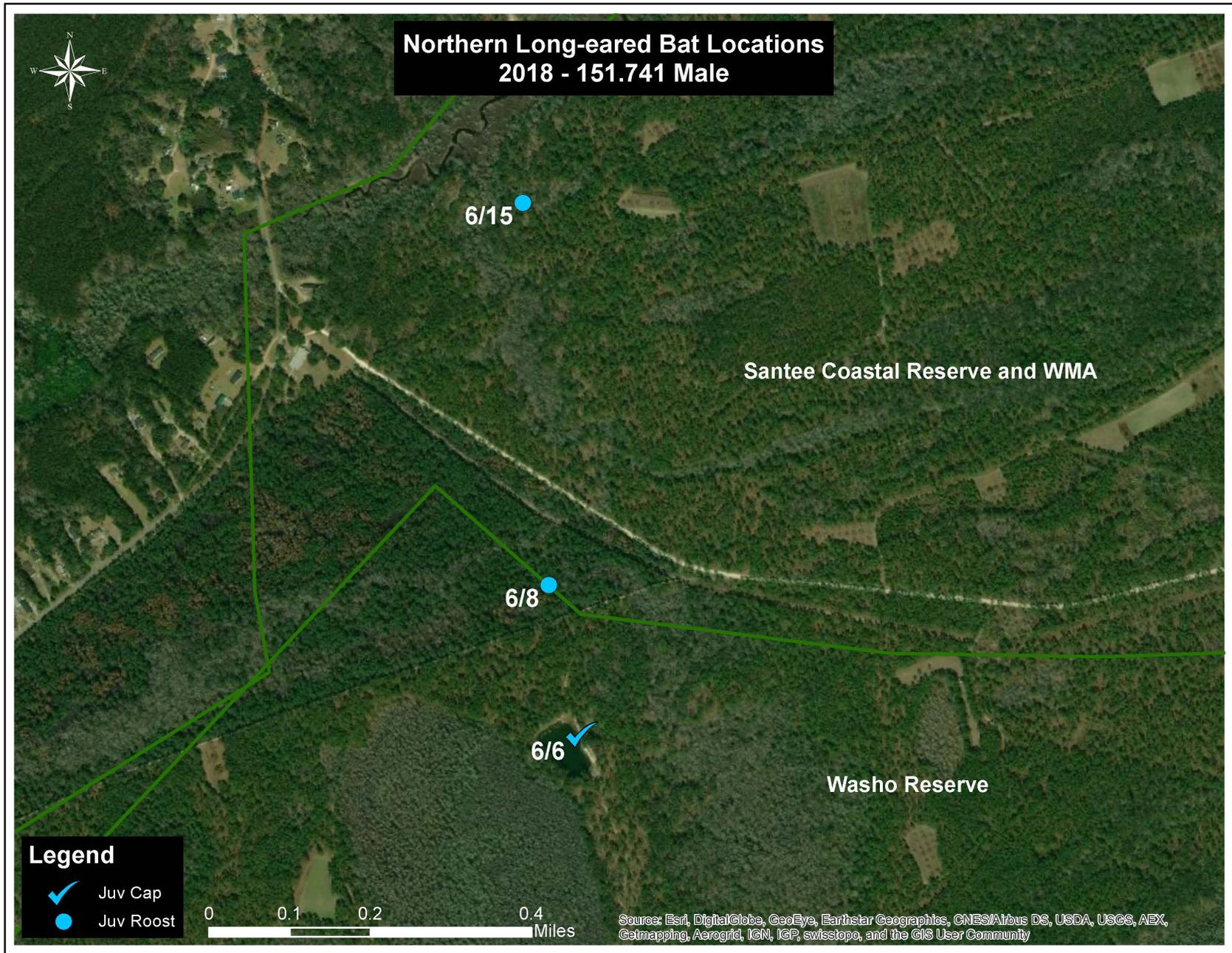
All female roosts on the property were within 150 feet of a gravel or dirt road. While it is unclear if individuals chose trees near a road, various warm sites have been known to be chosen by pregnant females to maximize growth of their pups requiring around 100 °F, and pines next to a road may be exposed to more sun. It should be noted that the subadult female in 2018 used similar roost types as the pregnant females, and her 5 roosts within 300 feet of each other were within 60 feet of a gravel road.

Though pregnant MYSE are known to form the largest colonies while pregnant, the pregnant females we tracked roosted alone or with only one other bat and no maternity colonies were recorded. However, a larger sample size may lead us to a maternity colony in the future. Biologists in North Carolina, who also captured pregnant MYSE for the first time on their coastal plain in 2019, found pregnant females roosting alone as well as in colonies. We estimate the pup season for this population to be between late April and early May, approximately one month earlier than the June 1 – July 31 pup season outlined in the current 4(d) rule. According to the USFWS, “For the northern long-eared bat, the 4(d) rule tailors protections to areas affected by white-nose syndrome during the bat’s most sensitive life stages. The rule is designed to protect the bat while minimizing regulatory requirements for landowners, land managers, government agencies and others within the species’ range.” We are discussing the possible inclusion of an earlier pup season in the 4(d) rule with the US Fish and Wildlife Service.

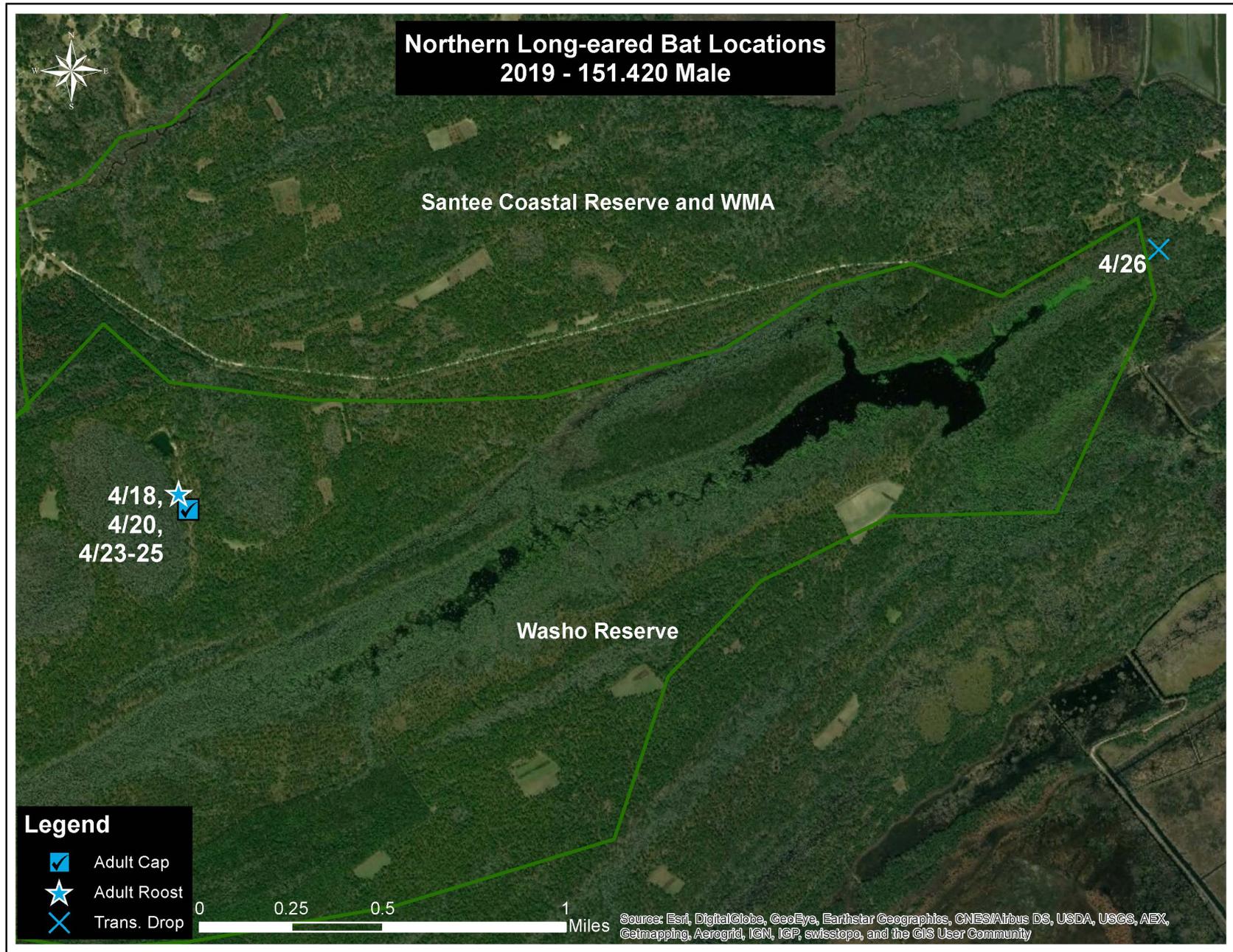
Frequent fire likely plays an important role for MYSE. Fire has beneficial effects on bat habitat as it reduces vegetative clutter, creates forest openings and snags, and potentially increases numbers of flying insects. However, the direct impacts of fire on bats and their roosts on the coastal plain, especially during the pup season, is unknown.

Negative results for *Pd* continues to be good news for bats on our coastal plain. *Pd* attacks bats while they’re hibernating and causes WNS and starvation, so if populations of Northern long-eared bats can forage on South Carolina’s warm coast during winter, their mortality from WNS could be greatly reduced. Understanding the extent, roost site characteristics, maternity colony locations, and timing of pups for coastal populations will help inform management for this WNS-affected species in coastal areas where they seem to be surviving thus far. As surveillance for *Pd* on our SC coast continues, we hope to provide insight into how our coastal Northern long-eared bat population is faring compared to heavily WNS-impacted northern populations.

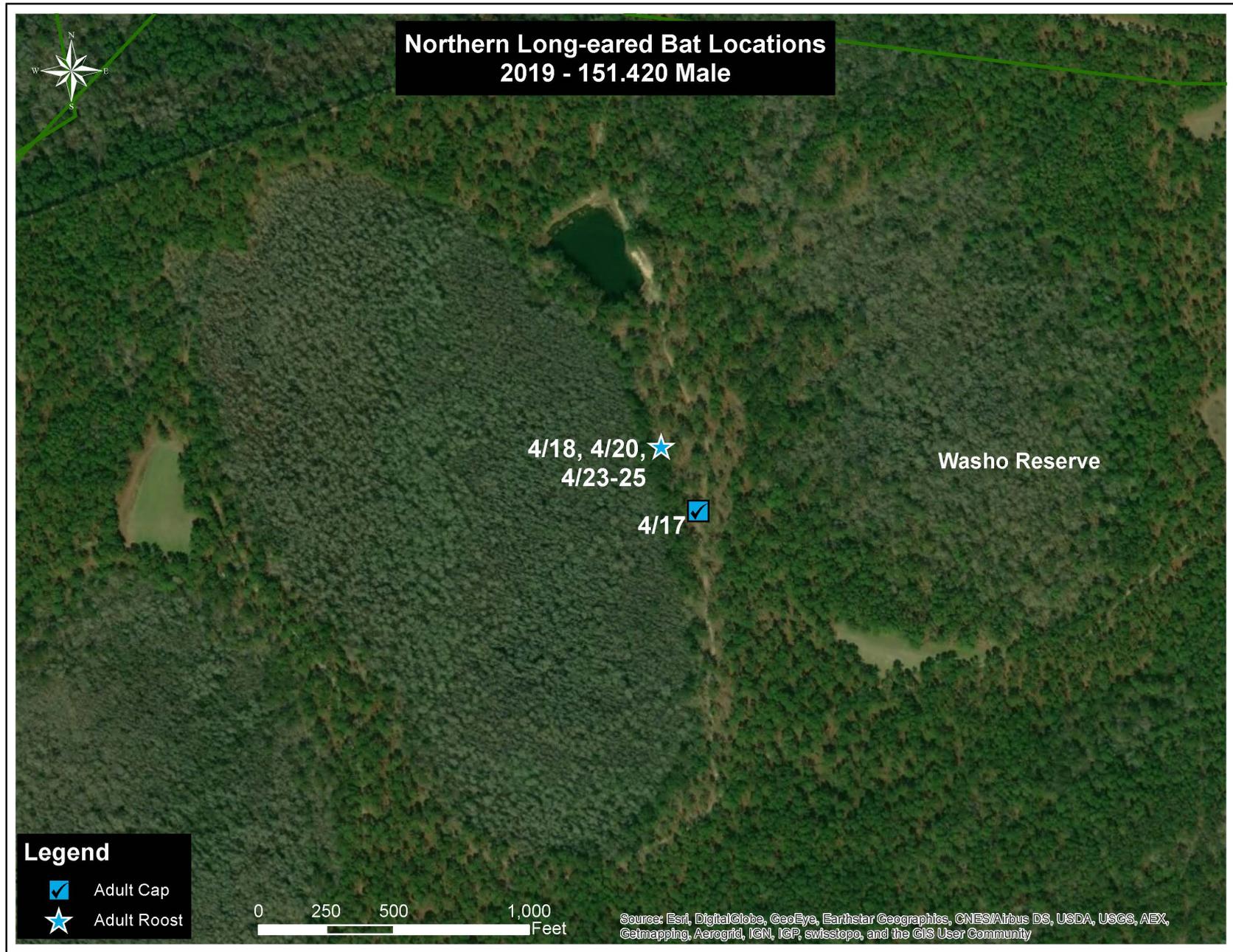
Appendix A: Locations of subadult male 151.741. Locations on 6/8 and 6/15 were approximate.



Appendix B: Locations of adult male 151.420.



Locations of adult male 151.420 main cavity roost (blue star) and capture site.



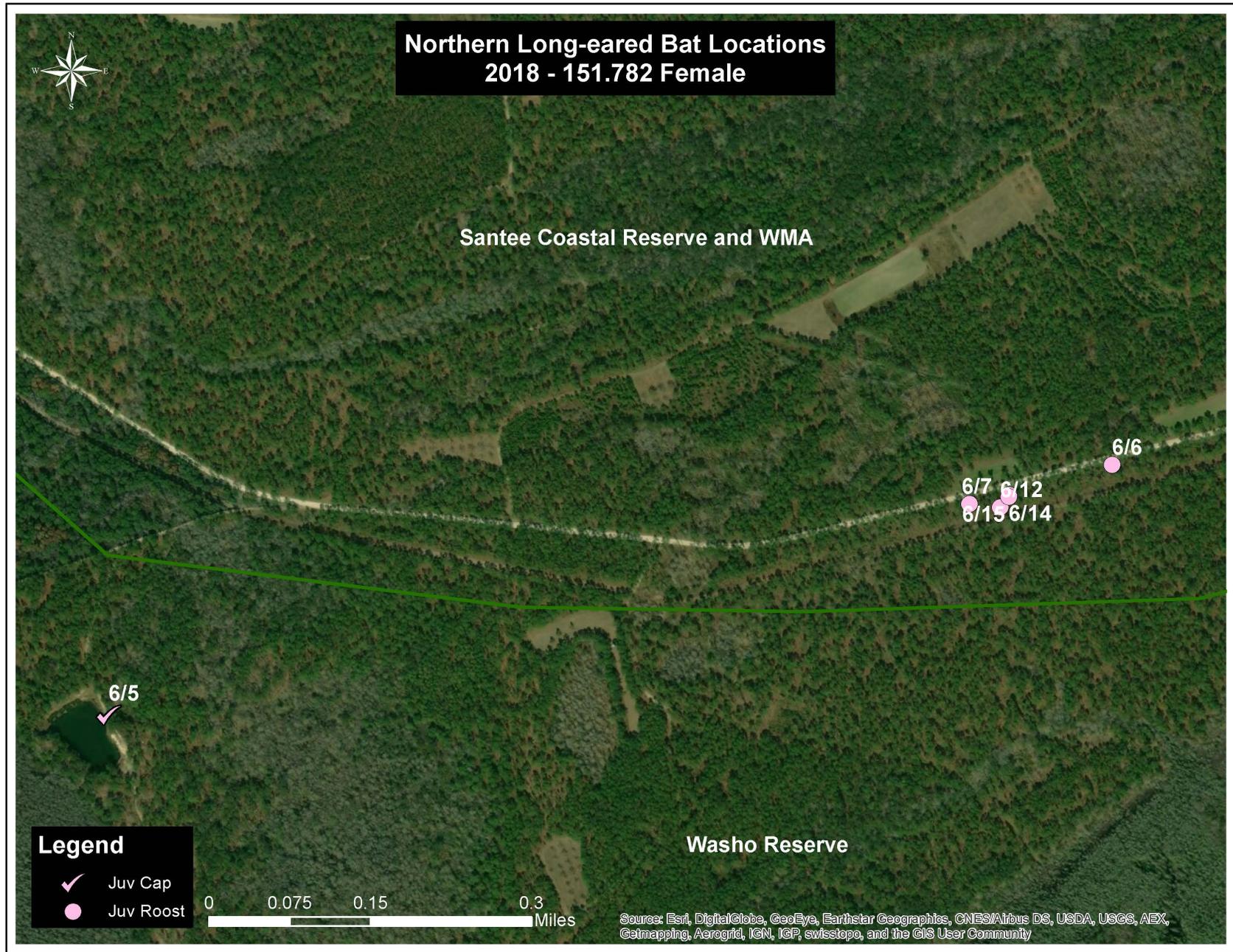
Locations of adult male 151.420 main cavity roost (blue star) and capture site, in detail.



Adult male 151.420 main roost in sweetgum tree cavity.



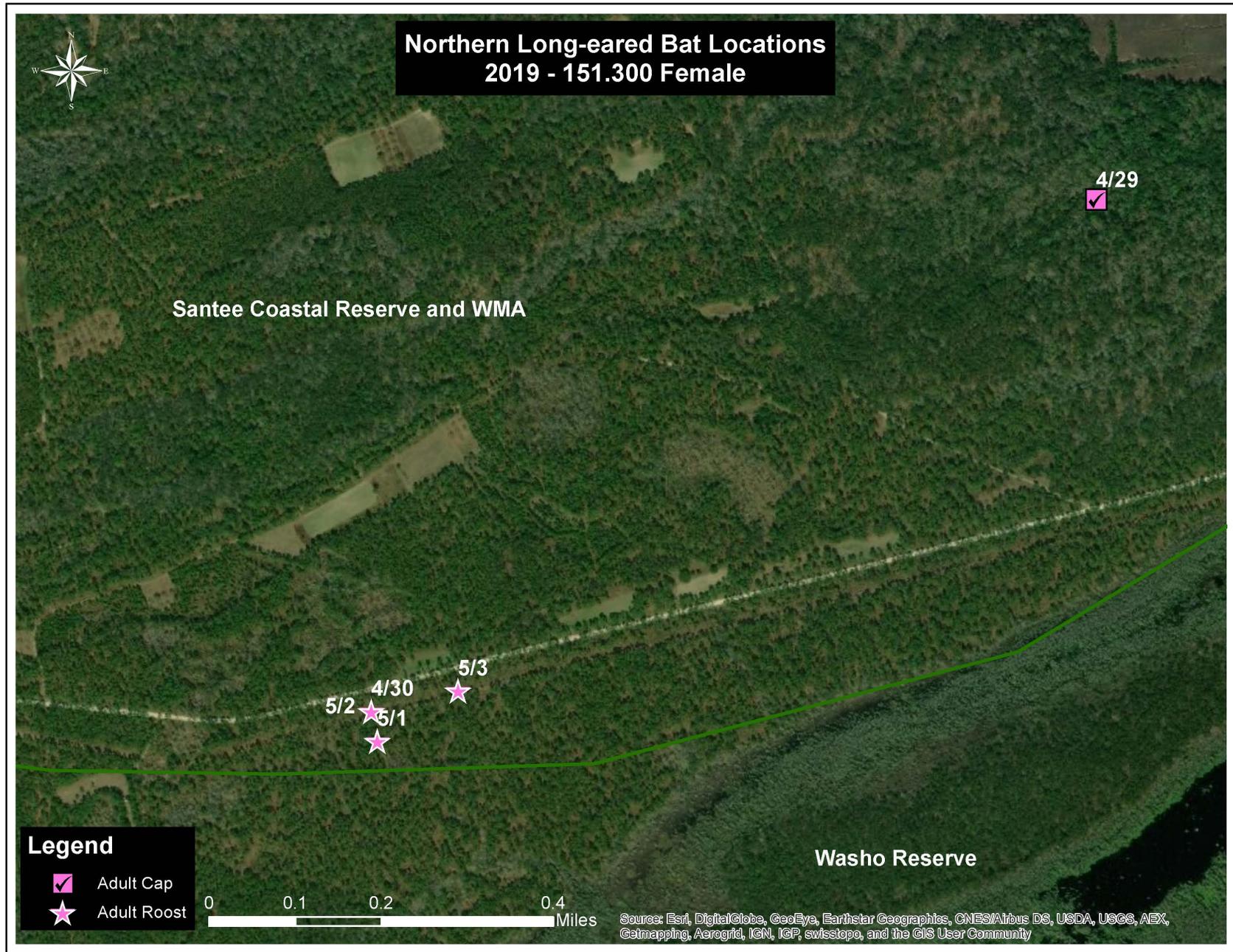
Appendix C: Locations of subadult female 151.782.



Roosts of subadult female 151.782, in detail.



Appendix D: Locations of pregnant female 151.300.



Roosts of pregnant female 151.300. Note all are within 150 feet from a road, and one roost tree was used twice.



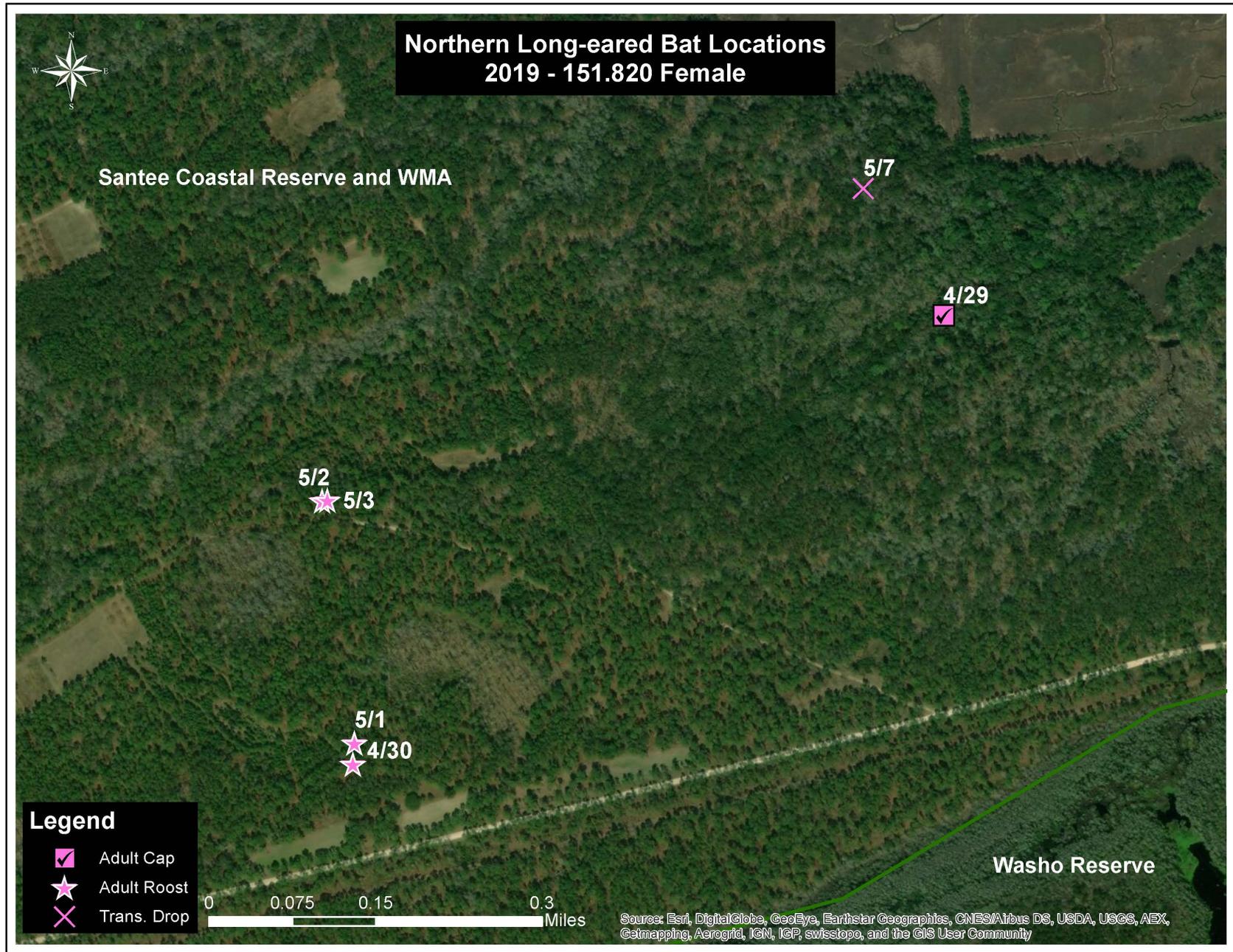
Pregnant female 151.300 roosts from 4/30 & 5/2, showing northeast side of roost.



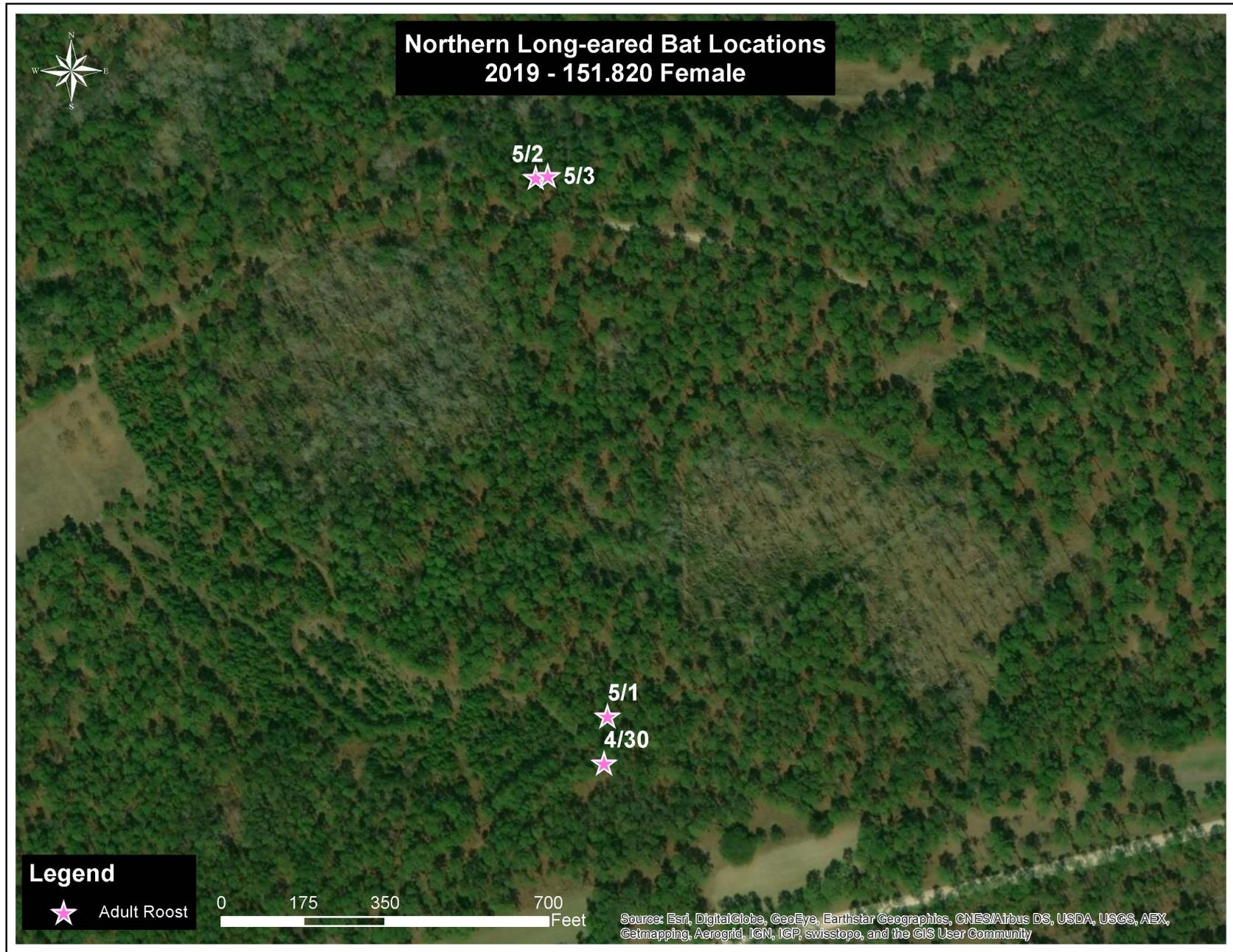
Pregnant female 151.300 roosts from 4/30 & 5/2, facing northeast toward road.



Appendix E: Locations of pregnant female 151.820.



Roots of pregnant female 151.820.



Pregnant female 151.820 roosts to the North. Note roosts are less than 100 feet from a road.



Pregnant female 151.820 roosts, showing south side of 5/2 & 5/3 roosts.



Pregnant female 151.820 roost, looking east-southeast at 5/2 roost from 5/3 roost.



Pregnant female 151.820 roosts to the South. Note roosts are less than 100 feet from a road (which runs between them)



Pregnant female 151.820 roost from 5/1, showing northeast side of roost. Note road in the back.



Pregnant female 151.820 roost from 5/1 roost, facing southwest toward roads.



South Carolina Department of Natural Resources



124 Wildlife Drive
Union, SC 29379

Robert H. Boyles, Jr.

Director

Emily C. Cope

Deputy Director for
Wildlife and Freshwater Fisheries

Sep 10th, 2020

Dear Wildlife Control Professional,

I am writing you/your company because you're listed on the SCDNR website as a wildlife control specialist that handles nuisance bats. This letter is being sent as a courtesy to help keep you informed on bat related issues in South Carolina. Attached are NWCOA recommended PPE Protocols and our bat ID guide. See below to access other documents digitally.

- In response to concerns regarding potential transfer of **COVID-19 from humans to bat populations**, the National Wildlife Control Operators Association (NWCOA) developed recommended Personal Protection Guidelines (PPE) for working with and handling bat populations. See <https://nwcoa.com/COVID-19-Updates>.
- The **September 13, 2018** version of the National WNS Decontamination Protocol continues to be the most recent. It can be found at www.whitenosesyndrome.org - select the heading "What Can I Do" and "Decontamination." Please consult this protocol for treating materials used on bat exclusions. Please do not move bat exclusion materials between states. Never move bats to new locations; you may accidentally speed the spread of WNS. Ten SC counties remain positive for either WNS or *Pd*. Oconee, Pickens, and Richland are WNS+ and Cherokee, Greenville, Lancaster, Laurens, Spartanburg, Union, York are *Pd*+ (WNS suspect; see our SC Bats website www.dnr.sc.gov/wildlife/bats and "White-Nose Syndrome" on the left menu). Other counties may be positive, so precautions will help prevent spreading the fungus between sites.
- The most updated **White-nose Syndrome fact sheet** is available at www.whitenosesyndrome.org - select "Multimedia and Education" and "Brochures, Postcards, and Fact Sheets." Select the fact sheet and select the attachment to download.
- **Acceptable Management Practices for Bat Control Activities in Structures** - A Guide for National Wildlife Control Operators is also available at www.whitenosesyndrome.org - search for "nuisance wildlife control" using the magnifying glass icon in the upper right-hand corner of the website.
- **Online Bat Standards courses** by National Wildlife Control Operators Association (NWCOA) are now being offered. Go to www.nwcoa.com and select Members. Under Upcoming Events you may see "Bat Standards Certified – Online" which you can select one to register. Otherwise, go to "Education" "Certifications" to view certifications and training.
- The fungus that causes WNS has been found on Brazilian free-tailed bats, a common bat found in buildings in SC. It is the only SC species with a tail that extends past the tail membrane. Evening and big brown bats are the other two species common in structures. If you see other species, please contact me and/or feel free to text me a picture (with face and ears visible) for ID help. Also see included bat ID guide (first two are also most common in buildings). **While bats can certainly be a nuisance, several species are in trouble because of WNS. With your help we can better monitor their populations.**
- The public can report known bat roosts, find out about SCDNR's citizen science project SC Bat Watch!, and view the SC Bat Conservation Plan at: <http://www.dnr.sc.gov/wildlife/bats/>.

Sincerely,

Jennifer Kindel

KindelJ@dnr.sc.gov

864-419-0739

HABITAT RELATIONSHIPS OF BAT SPECIES OF CONSERVATION CONCERN IN
COASTAL SOUTH CAROLINA

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
Wildlife and Fisheries Biology

by
Kyle Shute
August 2020

Accepted by:
David S. Jachowski, Committee Chair
Susan C. Loeb
Catherine B. Jachowski

ABSTRACT

Loss of forest habitat used for roosting and nocturnal activity by bats is a conservation concern in the southeastern United States. The northern long-eared bat (*Myotis septentrionalis*), southeastern myotis (*Myotis austroriparius*), tri-colored bat (*Perimyotis subflavus*), and northern yellow bat (*Lasiurus intermedius*) all occur within the Coastal Plain of South Carolina, where their greatest conservation threat is loss of critical roosting and foraging habitats. However, little research has been conducted on these species of conservation concern in this region, leaving gaps in information about habitat associations that would inform conservation and management as forest loss continues due to logging, agriculture, urban development, and intense storm events. To address this concern, we used radio telemetry and acoustic bat detectors to understand habitat associations of these species in southern coastal South Carolina. Our specific objectives were to 1) determine habitat characteristics associated with third order summer roost selection for the northern long-eared bat, tri-colored bat, and northern yellow bat, and 2) determine habitat characteristics associated with summer and winter nocturnal habitat use for *Myotis* spp., the tri-colored bat, and the northern yellow bat.

To understand summer roost selection, we radio-tracked individuals to roost trees May-August 2018 and 2019. We characterized roosts, roost sites, and associated available trees and used discrete choice models to analyze our data. Although we did not capture enough northern long-eared bats for resource selection analysis, we determined that one northern long-eared bat used bark roosts in slash pine (*Pinus taeda*) and one used basal cavities in water tupelo (*Nyssa aquatica*). Tri-colored bats and northern yellow bats

switched roosts frequently (every 1.3 days). Tri-colored bats used foliage and Spanish moss (*Tillandsia usneoides*) in hardwood trees and selected hardwood trees with high densities of Spanish moss. Northern yellow bats used dead palm fronds in cabbage palm trees (*Sabal palmetto*) or Spanish moss in hardwood trees and selected cabbage palm trees and trees with high densities of Spanish moss or dead palm fronds. Our results suggest that conservation of maritime and bottomland forests with trees that have high densities of roost structures would benefit all three species.

To investigate nocturnal habitat use we conducted acoustic surveys in summer (May-August) and winter (December-March) 2018 and 2019. We surveyed 125 sites in 5 habitat categories (upland forest, bottomland forest, fields, ponds, and salt marsh) in summer and 121 of these same sites in winter. We used occupancy models to analyze our data and interpreted results as habitat use. *Myotis* spp. used sites that were closer to hardwood stands and freshwater year-round, and sites closer to pine stands during winter. During summer, tri-colored bats were present at most sites (85%) and use was not dependent on any characteristics we measured, but during winter they used bottomland forests, fields, and ponds more than salt marsh and upland forests. During summer, northern yellow bats used sites close to freshwater and salt marsh, and used fields, ponds, and salt marsh more than upland and bottomland forests. During winter, they continued to use sites close to salt marsh and freshwater, but used bottomland forests, fields, and ponds more than upland forest and salt marsh. Our results highlight the importance of specific forest stands and features like freshwater, salt marsh, ponds, and bottomland

forests, while also highlighting that habitat use changes between seasons in response to resources and changes in vegetation structure.

DEDICATION

I dedicate this thesis to my parents and in memory of my grandparents. I could not have asked for a more loving family and you all mean the world to me. Putting me out in a canoe at six months old gave me an early start in caring about the natural world and it is something I will always be thankful for.

ACKNOWLEDGEMENTS

First and foremost, I thank Dr. Susan Loeb for her mentorship, patience, and support during my time at Clemson. The opportunity she has provided me has been invaluable to my professional development. I also thank Dr. David Jachowski, not only for his support but opportunities for banter, as well as Dr. Cathy Jachowski for engaging class discussion and analytical assistance whenever it was necessary.

This project would not have been possible without the financial support of the South Carolina Bat Monitoring and Research Project State Wildlife Grant and The Palmetto Bluff Conservancy. I extend my greatest appreciation to my contacts and collaborators Jennifer Kindel, Dr. Mary Socci, and Jay Walea for their field support and fruitful discussions. I also thank my collaborator Lydia Moore for her assistance in the field, discussions and feedback, but ultimately for her friendship. In addition to my collaborators, I thank my dedicated field technicians Kristen Van Neste and Vivian Steinbaugh for their hard work on this project as well as my graduate school cohort for providing a community of support while at Clemson. Finally, I thank my parents Lynne Flaccus and Greg Shute, as well as my partner Anthony Gray, who have always supported me and continue to do so every day.

TABLE OF CONTENTS

	Page
TITLE PAGE	i
ABSTRACT.....	ii
DEDICATION	v
ACKNOWLEDGMENTS	vi
LIST OF TABLES	viii
LIST OF FIGURES	ix
CHAPTER	
I. SUMMER ROOSTING ECOLOGY OF THREE BAT SPECIES OF CONSERVATION CONCERN IN COASTAL SOUTH CAROLINA	1
Introduction.....	1
Methods.....	5
Results.....	11
Discussion.....	14
Literature Cited	23
II. NOCTURNAL HABITAT USE OF BAT SPECIES OF CONSERVATION CONCERN IN THE CHANGING LANDSCAPE OF COASTAL SOUTH CAROLINA.....	36
Introduction.....	36
Methods.....	40
Results.....	46
Discussion.....	50
Literature Cited	58
APPENDIX.....	76

LIST OF TABLES

Table	Page
1.1 <i>A priori</i> models of tri-colored bat summer roost selection	28
1.2 <i>A priori</i> models of northern yellow bat summer roost selection	29
1.3 Average and standard deviation values of covariates for used and available trees.....	30
1.4 AIC _c table of summer roost selection models for the tri-colored bat and northern yellow bat.....	32
1.5 Coefficient estimate table of top models for tri-colored bat and northern yellow bat summer roost selection	33
2.1 <i>A priori</i> models for detection of target bat species	65
2.2 <i>A priori</i> models for <i>Myotis</i> spp. nocturnal habitat use and predictions for summer and winter	66
2.3 <i>A priori</i> models for tri-colored bat nocturnal habitat use and predictions for summer and winter	67
2.4 <i>A priori</i> models for northern yellow bat nocturnal habitat use and predictions for summer and winter	68
2.5 Confidence sets of target bat species detection models for summer and winter	69
2.6 Confidence sets of target bat species occupancy models for summer and winter	70
2.7 Coefficient estimates for top models of target bat species occupancy for summer and winter	71

FIGURES

Figure	Page
1.1 Map of study area.....	34
1.2 Relative probability of summer roost selection for the tri-colored bat and northern yellow bat as a function of tree group and roost structure density	35
2.1 Probability of <i>Myotis</i> spp. site occupancy as a function of distance to important landscape features	73
2.2 Probability of tri-colored bat and northern yellow bat site occupancy as a function of habitat type	74
2.3 Probability of northern yellow bat site occupancy as function of important landscape characteristics.....	75

CHAPTER 1: SUMMER ROOSTING ECOLOGY OF THREE BAT SPECIES OF CONSERVATION CONCERN IN COASTAL SOUTH CAROLINA

INTRODUCTION

Diurnal tree roosts are particularly important habitat features for bats as they provide protection from predators and adverse environmental conditions, and are sites for rearing offspring during the summer reproductive period (Carter and Menzel 2007). Roost structure use varies by bat species, but may be in foliage, bark of live or dead trees, and tree cavities. Bats select roost trees based on structural and landscape characteristics that meet their ecological needs (Kalcounis-Rüppell et al. 2005). Structural characteristics include roost tree diameter and decay status, canopy closure at the site, surrounding stand characteristics, and density of vegetative clutter around the roost (Lacki and Baker 2003; Carter and Menzel 2007), while landscape characteristics include factors like proximity to water, density of surrounding roost structures, and proximity to foraging areas (Lacki and Baker 2003; Kalcounis-Rüppell et al. 2005). Abundant roosts with preferred structural and landscape characteristics are important to meet the needs of entire populations and to facilitate switching of roosts by individuals. Individuals commonly switch roosts in response to changes in microclimate and roost availability, and to avoid predators and parasites (Lewis 1995; Lausen and Barclay 2002). Thus, an abundance of potential roosts that meet the needs of species is important to assure populations are sustained on the landscape.

Forest loss and consequently loss of roost trees, is a major conservation threat to bats and results from clear cutting, agricultural expansion, urbanization, and weather events intensified by climate change (Frick et al. 2019). The southeastern United States

faces many of these threats as it is projected to be a hotspot of natural forest loss (Poudyal et al. 2016) and to experience one of the largest urban expansions in the country (Terando et al. 2014). Loss of forests coupled with increasing intensity of storm events (e.g., hurricanes) due to climate change (Knutson et al. 2015; Ting et al. 2019) will likely result in high loss of roost trees. Loss of forests due to disturbance results in a matrix of varying quality habitat, separating animals from resources and in some cases leading to direct mortality (McKinney 2008; Russell et al. 2009). Loss of available tree cover also reduces the number of potential roosts that meet the needs of individual bat species, disproportionately impacting habitat specialists that rely on specific roost structures and leading to changes in roost selection (Loeb 2017). Changes in selectivity may cause bats to use suboptimal roosts, leading to decreased fitness, increased predatory exposure, and increased energy expenditure (Chaverri and Kunz 2011; Vlaschenko et al. 2019).

The northern yellow bat (*Lasiurus intermedius*), northern long-eared bat (*Myotis septentrionalis*), and tri-colored bat (*Perimyotis subflavus*) are species of special concern and occur in the Coastal Plain of the southeastern U.S. The northern yellow bat is relatively understudied throughout its range, with only a few studies documenting roost use (Constantine 1958; Menzel et al. 1999; Hutchinson 2006; Coleman et al. 2012). Northern yellow bats are associated with coastal maritime forests and roost in dead cabbage palm (*Sabal palmetto*) fronds and Spanish moss (*Tillandsia usneoides*) in the canopy of mixed hardwood trees such as *Quercus* spp. and *Nyssa* spp. (Menzel et al. 1999; Coleman et al. 2012; Castleberry et al. 2020). Castleberry et al. (2020), who conducted the only study on roost selection for this species, found that male northern

yellow bats select roosts in large trees with low surrounding clutter as well as sites that are close to freshwater when roost substrate is abundant on the landscape.

The northern long-eared bat was only recently discovered in the South Carolina Coastal Plain, expanding the known range of the species (White et al. 2018). Roost use varies across the range of this species but includes cavities and bark roosts in a variety of live and dead tree species (Carter and Feldhamer 2005; Perry and Thill 2007a; Garroway and Broders 2008). In portions of coastal South Carolina, northern long-eared bats roost under the bark of live pine trees (Confortin and Brown 2018; Kindel 2019). In contrast, tri-colored bats are a summer foliage roosting species and use roosts in hardwood leaves and pine needles, as well as in Spanish moss (Menzel et al. 1999; Veilleux et al. 2003; Perry and Thill 2007b; O’Keefe et al. 2009). In Nova Scotia, individuals select trees and sites with higher densities of beard lichen (*Usnea trichodia*) (Poissant et al. 2010), which provides similar roost characteristics as Spanish moss. Information on the roost ecology of the tri-colored bat in the southeastern Coastal Plain is limited, with only one published account of roost use by one individual (Menzel et al. 1999). Therefore, much information needs to be gained about roost use and selection of tri-colored bats in the Coastal Plain.

The northern long-eared bat and tri-colored bat have both experienced declines in their populations due to the disease white nose syndrome (WNS) caused by the fungus *Pseudogymnoascus destructans*. These declines have resulted in the northern long-eared bat being listed as threatened and the tri-colored bat being proposed for listing under the Endangered Species Act (USFWS 2017). WNS however, is not present in the Coastal Plain and thus, this area may serve as a refugia for both these species. Because all three

species face habitat conservation threats in the Coastal Plain, retention of important summer roosting habitat which facilitates survival and rearing of young is crucial to their persistence on the landscape. Thus, understanding summer roost selection of the northern long-eared bat, tri-colored bat, and northern yellow bat is important for informing conservation and management.

Our objective was to determine third order summer roost selection for the northern long-eared bat, tri-colored bat, and northern yellow bat in coastal South Carolina. We hypothesized that roost selection would vary by species but would be influenced by roost availability and permanence, surrounding forest cover type, thermoregulatory needs, ease of movement around the roost, landscape characteristics surrounding the roost, and anthropogenic disturbance. We predicted that northern long-eared bats would use pine trees and pine dominated stands while tri-colored bats would use oak species and northern yellow bats would use oak species and palm trees (Menzel et al. 1999; Kindel 2019; Castleberry et al. 2020). We also predicted that roost trees for the tri-colored bat and northern yellow bat would have high densities of potential roosting structures such as Spanish moss and dead palm fronds (Veilleux et al. 2003; Castleberry et al. 2020). Because of the importance of roosts in providing protection from the elements, we predicted that all species would select live roost trees that were protected by the canopy, but also that suit their energetic needs in terms of solar exposure and thermoregulation (Jung et al. 2004; Perry and Thill 2007a; Coleman et al. 2012; Kindel 2019). We also predicted that all species would use roost trees that were easy to maneuver around when coming in and leaving (Lacki and Schwierjohann 2001; Perry and

Thill 2007a; Castleberry et al. 2020) and that were close to landscape resources such as freshwater, foraging areas, and roads for commuting (Jung et al. 2004; Veilleux et al. 2004; Perry et al. 2008; O’Keefe et al. 2009; Castleberry et al. 2020). Finally, we predicted that tri-colored bats and northern yellow bats would roost at sites close to human disturbance which provides landscape heterogeneity with forests and open areas for roosting and foraging, while the northern long-eared bat would roost far from residential cover in order to avoid disturbance (Veilleux et al. 2004; Perry et al. 2008; Castleberry et al. 2020). Results of this study will provide a better understanding of roosting requirements and will inform land managers about critical habitat features for all three species.

METHODS

Study Area

This study took place at three properties in Beaufort County (32.35, -80.69) in the southern Coastal Plain of South Carolina: Palmetto Bluff, Pickney Island National Wildlife Refuge, and Victoria Bluff Heritage Preserve (Figure 1). All three study areas were located within the United States Southeast climate region (Karl and Koss 1984), which in the summer survey period (May-August) had a 20-year average temperature of 26.2°C and an average total precipitation of 52 cm (NOAA 2020). Palmetto Bluff (5,165 ha) is a multi-use property which is made up of suburban development including golf courses, maintained fields, and freshwater ponds, undeveloped land, and areas under conservation easement (132 ha). Forests were predominantly upland forest including pine dominated forests, mixed pine-hardwood forests, and maritime forest, with patches of

bottomland forest. Victoria Bluff (470 ha) is a state preserve which was undeveloped but bordered by suburban housing development and salt marsh. Dominant forest types at this study area were bottomland hardwood and mixed hardwood-pine forests. Pinckney Island is a National Wildlife Refuge (1,640 ha) surrounded entirely by salt marsh and in proximity to suburban development on the adjacent Hilton Head Island. Maritime forests made up most of the forest cover with patches of fields and ponds across the island.

Mist Netting and Tracking

We captured bats in mist-nets from May to August 2018 and 2019 on Palmetto Bluff, Victoria Bluff Heritage Preserve, and Pinckney Island National Wildlife Refuge. In 2018 we placed two triple high mist-net pole sets (Bat Conservation and Management, Inc. Carlisle, PA) at each net site along flight corridors including closed canopy roads, trails, and ephemeral wetlands. In 2019 we used the same triple high set up and opportunistically placed double high sets when possible. We used mist-nets that were 6 m, 9 m, and 12 m wide. We selected sites based on previous acoustic and capture records to increase probability of capturing target species. We opened nets 10 minutes after sunset and kept them open for at least 4 hours unless inclement weather prevented netting. We checked nets every 8-10 minutes, removed and identified each bat to species, and recorded weight, age class (adult or juvenile) based on joint ossification, forearm length, sex, reproductive condition, injury, and documented presence of any parasites; we banded individuals when possible. We classified females as non-reproductive, pregnant, lactating (visible milk under skin), or post-lactating (no visible milk and nipple bare), and males as non-reproductive (testes not descended) or reproductive (testes descended).

We affixed radio transmitters to the interscapular region of tri-colored bats during 2019, and northern long-eared bats and northern yellow bats during 2018 and 2019. We used 0.27 g LB-2X transmitters on tri-colored bats, 0.31g LB-2X transmitters on northern long-eared bats, and 0.52 g LB-2 transmitters on northern yellow bats (Holohil Systems, Ontario, Canada). We trimmed fur, cleaned the area with alcohol, and used surgical adhesive (OSTO-BOND, Montreal Ostomy, Quebec, Canada) to attach the transmitter. Transmitters were $\leq 5\%$ of the bats' body weights and all handling and tagging procedures were conducted in accordance with the American Society of Mammalogists' guidelines (Sikes et al. 2016) and approved by the Clemson University IACUC (#2017-072) and U.S. Forest Service IACUC (#2018-002).

The day following radio-tagging and all subsequent days, we attempted to track individuals to their roost tree using a receiver (Wildlife Materials, Murphysboro, IL) and 3 or 5 element antenna. If we could not locate an individual, we attempted to determine if it was still in the area by listening for its transmitter frequency at night and identifying the direction it was coming from to aid in the roost search the next day. We stopped looking for an individual if we could not detect it for 5 days. If a roost was located on private property, we gained permission from the landowner to access their property. We marked each roost tree using an aluminum tag and recorded its location using a Trimble GeoExplorer 2008 Series Global positioning System unit (Trimble Inc., Sunnyvale, CA) and attempted to visually confirm the roost structure. When we could not visually confirm a roost, we determined the most likely roost tree and conducted emergence surveys when possible to locate the roost structure.

We identified each roost tree to species, measured the diameter at breast height (DBH) and tree height, and determined its canopy position (below canopy or not). For analysis we grouped roost tree species into categories (*Pinus* spp., *Quercus* spp., and other for tri-colored bats and *Quercus* spp., *Sabal*, and other for northern yellow bats); we did not group tree species for northern long-eared bats. For tri-colored bats and northern yellow bats we established a transect along a randomly selected bearing from one edge of the roost tree canopy to the opposite edge, intersecting the middle of the plot. We measured canopy diameter along this transect and counted number of Spanish moss clumps that intersected the transect and were large enough to conceal a roosting bat. We created a 0.05 ha (radius = 12.5 m) circular plot around each roost tree and measured DBH of all trees ≥ 10 cm DBH and identified each to genus to estimate relative abundance of different tree groups. Additionally, we measured canopy closure at the roost tree and 6 m from the tree in each cardinal direction using a spherical densiometer (Model-A, Forest Densimeters, Forestry Suppliers Inc., Jackson, MS) and averaged these to obtain a canopy closure value for the plot. We also measured distance to nearest tree and distance to nearest tree taller than the roost tree. To characterize midstory stem density, we established a 25 m transect through the plot center along the same randomly selected bearing as used to quantify Spanish moss and counted all stems ≥ 4 cm DBH and < 10 cm DBH within 1 m of either side of the transect. We used ArcMap (10.5.1) to calculate distance to the nearest freshwater pond, distance to the nearest road (paved or unpaved), distance to salt marsh, distance to forest edge, distance to residential area, and proportion of forest within 165 m (Broders et al. 2006); we assigned cover type based on

the SCGAP raster (SCDNR 2001). Even though this is an older database we used it because it most accurately represented forest cover type compared to other databases.

We created a buffer around each roost tree with a radius equal to either the farthest distance an individual of the species moved between roosts or from the capture site to first roost tree, whichever was greater (northern yellow bat radius = 1.08 km, northern long-eared bat radius = 1.90 km, tri-colored bat radius = 4.25 km). This gave us an estimate of the area potentially available to a bat during nightly movement. We took this approach because of limited information on home range size or nightly movements of these species in this region. Within each buffer we generated 10 random points using the ArcMap extension Alaska Pak version 3.0.0 (NPS 2010). For each roost occasion (i.e., day that a bat used a tree), we selected one random tree for the northern long-eared bat (1:1) and two random trees for the tri-colored bat and northern yellow bat (1:2). To select these trees, we randomly ordered the available points and selected the first two for northern yellow bats and tri-colored bats and first one for the northern long-eared bat because of time constraints. If more than one roost occasion occurred at a tree, we progressively selected the random points until we had chosen enough available trees for the number of roost occasions. When random points fell in salt marshes or ponds where there were no trees, we removed the point and moved to the next one. At each selected random point, we searched for the closest available tree to the point (usually within 10 m) and collected all habitat measurements outlined above for the used roost tree. For northern yellow bats available trees were 1) live broadleaved hardwood trees ≥ 10 cm DBH, or 2) live cabbage palm trees (*Sabal palmetto*) ≥ 6 m in height. For tri-colored bats

available trees were 1) live hardwood trees ≥ 10 cm DBH, or 2) live pine trees ≥ 10 cm DBH. For northern long-eared bats available trees were 1) hardwood trees ≥ 10 cm DBH with or without a basal cavity, or 2) pine trees ≥ 10 cm DBH. We defined availability for each species based on the roost structures that were used by each.

Analysis

Based on previous literature, we developed six a priori models based on influence of roost availability, forest cover type, thermoregulation and roost permanence, movement ability around the roost, surrounding landscape resources, anthropogenic disturbance on tri-colored bat (Table 1) and northern yellow bat (Table 2) roost selection. We also fit a subglobal roost characteristics model and subglobal landscape characteristics model. Due to small sample size we were unable to conduct roost selection analysis for the northern long-eared bat. We scaled all continuous covariates prior to analysis and screened for correlation of continuous covariates. We used discrete choice models in R package “mlogit” (Croissant 2019) to analyze our data where response variables were choice sets made up of one used tree and two available trees for each roost event. We ranked models using Akaike’s Information Criterion corrected for small sample size (AIC_c), and defined the confidence set of top models as those with $\Delta AIC_c \leq 4$. We defined important covariates by 85% confidence intervals that did not overlap zero (Arnold 2010). We used our top model for each species to conduct 10-fold cross validation using 80% of our data to train the model and the remaining 20% to test the model (Boyce et al. 2002). We present proportion of test data choice sets in which the model correctly identified the used tree. For these proportions, 1.0 indicates perfect performance of the model and 0.50 indicates that the model performed no better than

random. We present covariate values as $\bar{x} \pm SD$. We used Program R version 3.6.1 (R Core Team 2019) for all analyses.

RESULTS

We mist-netted 32 nights in 2018 and 26 nights in 2019. In 2018 we captured 170 bats: 46 tri-colored bats, 41 evening bats (*Nycticeius humeralis*), 39 seminole bats (*L. seminolus*), 29 big brown bats (*Eptesicus fuscus*), eight eastern red bats (*L. borealis*), five southeastern myotis (*M. austroriparius*), one northern long-eared bats, and one northern yellow bat. In 2019 we captured 151 bats: 36 tri-colored bats, 35 evening bats, 32 seminole bats, 32 big brown bats, six eastern red bats, five northern yellow bats, three northern long-eared bats, and two southeastern myotis.

We radio-tagged and tracked two non-reproductive adult male northern long-eared bats at Palmetto Bluff. When we were able to conduct roost emergences or visually confirm the individual in the roost, we only observed bats roosting solitarily. One northern long-eared bat was captured and tracked in both 2018 and 2019 and one was captured and tracked in 2019. We tracked northern long-eared bats for an average of 7.3 ± 1 days (range 6-8) and identified seven roost trees. Northern long-eared bats stayed in roosts for 2.2 ± 1.7 days (range 1-5) and the mean distance between subsequent roost trees was 224 ± 187 m (range 67-533). The individual that we tracked in 2018 and 2019 used live slash pines (*P. elliotii*) as roosts in both years, two in 2018 and three in 2019. The other bat used two live water tupelo (*Nyssa aquatica*). All roosts in the slash pine were under bark, and those in water tupelo were in cavities with basal openings, one of which had a cavity opening that was approximately 3 m tall. On average, canopy closure

surrounding roost trees was slightly (1.08 times) higher than around random trees, but tree height, DBH, plot basal area, and number of midstory stems were similar between roost and random trees (Table 3). Distances to various landscape features were highly variable among used and available trees; however, on average roost trees were slightly closer to freshwater (1.4 times closer) and roosts had a slightly higher average proportion of forest (1.08 times higher) within 165 m than random trees (Table 3).

We radio-tagged and tracked seven tri-colored bats (one juvenile female, two juvenile males, three adult females, and one adult male) for an average of 4.5 ± 2.5 days (range 1-9). Five bats were captured and tracked at Palmetto Bluff and two at Pinckney Island National Wildlife Refuge. We tracked bats to 25 roost trees (3.8 ± 2.3 roost trees per bat, range 1-8). Tri-colored bats spent 1.3 ± 0.5 days (range 1-3) in a roost and average distance between subsequent roosts was 107 ± 84 m (range 6–294 m). Used tree species were live *Liquidambar styraciflua* (n = 7), *Quercus virginiana* (n = 7), *Celtis laevagata* (n = 3), *Q. laurifolia* (n = 2), *Q. nigra* (n = 2), *Acer rubrum* (n = 1), *Magnolia grandiflora* (n = 1), *M. virginiana* (n = 1), and *P. taeda* (n = 1). We visually confirmed use of Spanish moss and dead foliage roosts for this species and did not find evidence that tri-colored bats used roosts other than foliage. Of the 25 roosts, we confirmed that 13 were in Spanish moss, two were in dead foliage, and nine were in unidentified roosts that we presumed were Spanish moss because of high density of it on the tree and there were no other apparent roost structures; one roost was in an unknown foliage roost (presumed dead foliage). We only observed bats roosting alone. On average, DBH, canopy closure, and density of Spanish moss were higher (1.30, 1.18, and 7 times higher respectively) in

used trees than available trees (Table 3). Used sites on average had lower proportion of pine trees (2.20 times lower) and higher proportions of oak trees in the surrounding plot than available (1.79 times higher); distance to all landscape features was highly variable between used and available trees (Table 3). Distance to residential areas ranged from within residential yards to almost 1.6 km away.

We modeled tri-colored bat roost tree selection from 32 choice sets. The roost structure availability model was the top model and carried 0.94 of model weight (Table 4). Important covariates in this model were *Pinus* spp. and Spanish moss density (Table 5). Relative probability of selection was negatively related to *Pinus* spp., indicating that tri-colored bats avoided pine trees, and positively related to Spanish moss density (Figure 2a). The proportion of test cases where the model correctly identified the true roost was 0.83 indicating that our model correctly predicted the used tree 83% of the time.

We radio-tagged six adult male northern yellow bats and tracked them to 27 trees (one bat to seven trees in 2018 and five bats to 20 trees in 2019) for an average of 4.5 ± 2.9 (range 1 – 12) trees per bat. We tracked northern yellow bats for an average of 9.2 ± 5.4 days (range 1-12) and they spent 1.3 ± 0.6 days (range 1-3) per roost tree. Average distance between subsequent roosts was 299 ± 284 m (range 52–1078). Used trees were live *S. palmetto* (n = 12), *Q. virginiana* (n = 6), *N. aquatica* (n = 3), *Q. laurifolia* (n = 3), *Q. nigra* (n = 2), and *Q. chapmanii* (n = 1). We visually confirmed use of Spanish moss for three individuals and dead palm fronds for two. Of the 27 roosts, 12 were in dead cabbage palm fronds, seven were in Spanish moss, and eight were in canopy roosts that we presumed were in Spanish moss because of density of Spanish moss on the tree and

there were no other apparent possible roost structures. All individuals that we observed appeared to be roosting alone. Individuals were consistent in use of one roost tree type and we did not document individuals switching between Spanish moss or foliage roosts in hardwood trees and dead palm fronds. On average, used trees had variable but slightly larger DBH (1.32 times higher), higher canopy closure (1.17 times higher), and were similar in height to those that were available (Table 3). Density of roost structures on used trees was higher than on available trees (5.66 times higher) and proportion of pine trees in the surrounding plot was lower at used trees than available ones (1.56 times lower) (Table 3). Distance to landscape features was variable, but on average used trees were marginally closer to freshwater, salt marsh, and residential cover (1.29, 1.47, 1.80 times closer respectively) (Table 3). Distance to residential area ranged from within residential yards to approximately 370 m away.

We modeled northern yellow bat roost selection from 37 choice sets. The roost structure availability model was the top model holding 0.93 of model weight (Table 4). Important covariates in this model were *Sabal* spp. and roost structure density (Table 5). Relative probability of selection was positively related to *Sabal* spp. and roost structure density (Figure 2b). The proportion of test cases where the model correctly identified the true roost was 0.84 indicating that our model correctly predicted the used tree 84% of the time.

DISCUSSION

We found that roost structure abundance and tree species, as opposed to landscape characteristics, was important in determining roost selection for both tri-colored bats and

northern yellow bats. Across bat species, various tree characteristics, especially those associated with roost structures, are important in determining selection (Menzel et al. 2002; Kalcounis-Rüppell et al. 2005; Rhodes and Wardell-Johnson 2006; Perry and Thill 2007a; Poissant et al. 2010). When sites have high densities of roost structures, individuals have multiple options that they may choose from, providing the opportunity to select structures that best suit their ecological needs. It is possible that landscape features are important, but only when roost structures are evenly distributed or abundant across the landscape (Miles et al. 2006; Castleberry et al. 2020). Our roost selection results highlight that roost availability is likely limited to specific areas on the landscape.

The two northern long-eared bats that we tracked used different roost sites and forest types from each other but displayed some similar roosting behavior to other individuals in coastal South Carolina. The northern long-eared bat that we tracked in 2018 and 2019 used the bark of live *P. elliotii* trees which were in sites dominated by even aged pine. In contrast, the northern long-eared bat we tracked in 2019 used only *N. aquatica* with basal cavities in sites dominated by oak species. Use of both bark and basal cavity roosts have been reported elsewhere on the coast of South Carolina (Kindel 2019). Roost trees were similar in height and canopy closure between the individuals, but the pine roosts were smaller in diameter than the *N. aquatica*, likely due to the use of basal cavities which form in large, old trees. Canopy closure values for all trees in our study (on average 90%) were higher than other northern long-eared bat roosts in parts of the southeast (74.5% for males and 66% for females) (Perry and Thill 2007a), and much higher than roosts at higher latitudes (41%) (Jung et al. 2004). Many species of bats

select roosts with lower canopy closure to maximize solar exposure (Fabianek et al. 2015). It is possible that at lower latitudes where temperatures are higher, solar exposure is not as important to roost use.

Over the course of our study we did not capture any female northern long-eared bats, and only three males, one of which was too small to affix a transmitter to. One individual either remained resident or returned to the same area between years (capture site in 2019 was about 350 m from 2018 roost trees), but overall, we still know very little about the reproductive and population ecology of this species in the region. Populations in our study area are at the southernmost extent of the known range along the Atlantic coast (White et al. 2018) and it is possible that this species is in low numbers at the periphery of the range. Additionally, individuals may be impacted by habitat fragmentation around our study areas making it difficult to colonize from other patches (Bennett and Saunders 2010; Chaverri and Kunz 2011).

While tri-colored bats in our study did not select oak trees over other species as observed in Veilleux et al. 2003, they did avoid pine trees and selected roost trees that had high densities of Spanish moss in line with our predictions. Broadleaved trees not only provide adequate structure for Spanish moss to grow (Garth 1964), they also provide dead foliage clumps, both of which can be used for roosting (Menzel et al. 1999; Veilleux et al. 2003). Tri-colored bats in Nova Scotia select roost trees and roost areas that have high densities of *Usnea trichodia*, a lichen that provides similar structure to Spanish moss (Poissant et al. 2010). Although we did not quantify amount of Spanish moss in trees surrounding roosts for our analysis, Spanish moss is likely to be present in stands

surrounding a colonized tree because it spreads to neighboring trees from colonized ones (Garth 1964).

Tree and site characteristics used by tri-colored bats in our study varied from those used in other parts of the species range. Individuals that we tracked used trees with slightly higher percent canopy closure (85%) and larger DBH (52.4 cm) than available and had higher values than reported by other studies (58% and 24.3-26.5 cm respectively) (O'Keefe et al. 2009; Poissant et al. 2010). Bats that roost in sites with low canopy closure may experience warmer temperatures due to more solar exposure, which helps save energy if they take advantage of passive rewarming (Turbill et al. 2003). Alternatively, sites with high canopy closure may better insulate roosting bats from sun exposure (Veilleux et al. 2004) which may be useful at low latitudes where temperatures are high. Although not an important covariate in our selection analysis, the proportion of oak trees in the area surrounding roost trees was higher than around available trees. These results are similar to those of Veilleux et al. (2003) who found preference for roost trees in forests that had more oaks.

As we predicted, relative probability of selection by northern yellow bats was higher for cabbage palm trees compared to other tree groups and increased with density of Spanish moss or dead palm fronds. While relative probability of selecting oak trees was not different than other trees, we think oaks may be important because they accounted for 44% of used trees and were used the majority of the time in other study areas (Menzel et al. 1999; Coleman et al. 2012; Castleberry et al. 2020). Oaks and cabbage palms as well as other hardwoods provide roost structures like Spanish moss and

dead palm fronds that may benefit this species. Dead cabbage palm fronds and Spanish moss match the coloration of the northern yellow bat and thus, likely provide camouflage from predators. These structures may also protect individuals from storms by repelling rain and keeping the bat dry (Hutchinson 2006; Castleberry et al. 2020). While it is still unclear why some individuals used only Spanish moss or hardwood foliage roosts and others used only dead palm fronds, individuals never overlapped in the use of both roost structures. Exclusive use of a single structure may be a result of intraspecific competition; however, it does not seem that structures were limited on the landscape given apparently low population sizes of northern yellow bats, or other species that use Spanish moss in relation to its abundance on the landscape.

Our results differed in some ways from the other roost selection study on northern yellow bats in Georgia. Castleberry et al. (2020) found that roost tree DBH was higher than surrounding trees and while on average, DBH of roost trees in our study was slightly higher than available trees (Table 3), roost trees were highly variable in diameter (range 16.4-164.1 cm). Northern yellow bats in Georgia also select trees with more clearance below the roost than below available trees. We did not measure clearance directly below roosts, but midstory density, which would reflect similar open flight space around the roost tree, was not different between used and available trees.

Counter to our predictions, we found that landscape features were not important in determining roost site use and selection for any species. Other studies indicate that proximity to landscape features, such as freshwater, roads, and nearby roosts, are important in roost selection (Veilleux et al. 2004; Perry et al. 2008; O'Keefe et al. 2009;

Poissant et al. 2010; Castleberry et al. 2020). We observed that on average northern yellow bats roosted closer to freshwater, salt marsh, and residential areas, and that northern long-eared bat roost trees were always surrounded by > 92% of forest within 165 m. Features like freshwater, salt marsh, and various forest stands provide access to drinking water, foraging areas, and alternate roosts, but may be secondarily important to abundance of roost structures and specific roost trees (Miles et al. 2006). Castleberry et al. (2020) suggested that landscape features may only be important when roost structures are ubiquitous across the landscape. The importance of roost structures relative to surrounding characteristics may explain why our landscape model did not receive support in the selection analysis. If specific roost structures (e.g., Spanish moss or palm fronds) are not available equally across the landscape, individuals may not have the flexibility to select sites close to important landscape features, highlighting that selection is a hierarchical process (Johnson 1980). It is also possible individuals in our study were able to efficiently commute to important landscape resources such as foraging areas and freshwater, reducing the need to roost close to them. In our study area, features like freshwater and fields (which could be used for foraging by the tri-colored bat and northern yellow bat) were distributed relatively homogeneously and in some cases in close proximity to one another. Even distribution of these landscape features and close proximity to one another may limit the need for bats to select roosts close to these features. Finally, it is also possible that the buffers which we used to measure availability did not capture sufficient variability in distances to landscape features. Other studies on these species quantified availability at the landscape scale by placing points across the

whole study area (Castleberry et al. 2020), likely capturing more variation in the landscape and as a result, were able to detect patterns of landscape scale roost selection. However, quantifying availability without using species movement metrics may overestimate what is available to individuals.

Contrary to our prediction, we also did not find evidence that individuals of any focal species avoided residential development when selecting roosts. Some northern yellow bats roosted in residential yards, some tri-colored bats roosted next to ongoing construction, and two northern long-eared bat roosts were < 300 m from ongoing construction. Low-density housing that retains forest patches may leave appropriate roosts for some species even within urbanized areas (Rhodes and Wardell-Johnson 2006). However, differences in response to urbanization are likely related to not only species-specific roost characteristics, but also degree of urbanization. Housing density and disturbance in our study area may not have been high enough to impact the three focal species. However, roost selection that occurs within a gradient which includes a more developed urban area may be impacted by development density because urbanization can negatively impact bats (Frick et al. 2019).

Our study provides important ecological information for species that are understudied in this region. However, habitat selection of females, particularly reproductive ones, is not well understood for all these species in the Coastal Plain. For example, other studies on the northern yellow bat have also captured few females (Coleman et al. 2012; Castleberry et al. 2020). In addition, the small number of pregnant northern long-eared bats that have been tracked elsewhere on the coast of South Carolina

used roosts with much lower canopy closure (20-60%) than the males in our study (90%) (Kindel 2019) which may relate to differing physiological needs and torpor patterns between sexes (Grinevitch et al. 1995). Because habitat selection may vary by demographic and reproductive group (Veilleux et al. 2004; Perry and Thill 2007a) conducting selection studies for these groups separately, as well as further investigation of reproductive periods and population dynamics in this region is critical.

All three species switched roosts multiple times during tracking periods, although northern long-eared bats switched roosts less frequently than tri-colored and northern yellow bats, which switched roosts almost every day. Additionally, the tri-colored bats and northern yellow bats we tracked switched roosts more frequently than reported by others (O’Keefe et al. 2009; Coleman et al. 2012). Switching roosts is a tactic to reduce parasite loads and predation risk, and to access more suitable microclimates (Lewis 1995; Lausen and Barclay 2002). In addition, switching roosts frequently may relate to roost permanence and potential loss of roosts (Lausen and Barclay 2002). If some roost structures are impermanent (e.g., foliage roosts like Spanish moss or dead foliage), adaptations that facilitate the ability to use multiple roosts would benefit individuals by allowing them to be flexible when roosts are lost. While reuse of trees occurred sporadically, northern yellow bats and tri-colored bats typically used new trees in proximity to old ones, displaying fidelity to an area as opposed to a specific tree. This has been documented in foliage roosting species, and specifically in other tri-colored bat and northern yellow bat populations (Veilleux and Veilleux 2004; Castleberry et al. 2020). Frequent roost switching in our study highlights the importance of the conservation of

forests that provide many suitable roost trees with adequate foliage and Spanish moss roost structures. Bats switch roosts when their physiological or ecological needs are not being met (Lewis et al. 1995) and thus the presence of many roost options nearby is important to their survival

Bat populations across the eastern United States face a variety of conservation threats. In the Coastal Plain of South Carolina, the predominate threat to bats is human disturbance. Loss of forests as a result of land use change removes critical roosting structures, ultimately impacting tree roosting species (Russo and Ancillotto 2014). By identifying features used by the northern long-eared bat, tri-colored bat, and northern yellow bat, we provide information for managers making decisions about how to manage land for these species. Overall, our results highlight the importance of roost structure availability and the conservation of bottomland and maritime forests with a diversity of hardwood trees that foster the growth of Spanish moss (Garth 1964) and dead foliage. Further, retention of dead palm fronds which are often removed for aesthetic purposes will leave more roost structures on the landscape for these species. Frequency of roost switching in our study further highlights the importance of conserving forest stands that have abundant roost structures for these species. Additional study on all these species in this region is needed to better understand habitat associations and how selection varies among demographic groups, particularly females. Given the species' declines elsewhere in their ranges, this information will allow for development of conservation strategies that retain critical habitat features for these species of special concern.

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TABLES

Table 1. A priori models for tri-colored bat roost selection at three study areas in the Coastal Plain of South Carolina in summer (May-August) 2018 and 2019.

Model	Covariate	Prediction	Citation
1. Roost Structure Availability	Roost Tree Category	Select for <i>Quercus</i> spp.	Veilleux et al. 2003
	Spanish moss density	Select for trees with higher Spanish moss density	Menzel et al. 1999
2. Cover Type	Stand Composition	Select for Maritime and Bottomland Forests	Perry et al. 2007, Menzel et al. 1999
3. Thermoregulation and Roost Permanence	Tree Dominance	Select for codominant trees	Veilleux et al. 2003
	Roost Tree DBH	Select for larger DBH trees	Castleberry et al. 2008
	Distance to Nearest Taller Tree	Select for trees closer to nearest taller tree	Veilleux et al. 2003
	Canopy Closure	Select for sites with low canopy closure	O'Keefe et al. 2009, Perry and Thill 2007a
4. Movement Ability	Midstory Stem Density	Select for sites with low midstory stem density	Veilleux et al. 2003
	Overstory Basal Area	Select for sites with higher overstory basal area	Perry and Thill 2007a
	Overstory Stem Density	Select for sites low overstory stem density	Perry and Thill 2007a
5. Landscape Resources	Distance to freshwater	Select for sites closer to freshwater	Veilleux et al. 2004
	Distance to edge	Select for sites closer to openings	O'Keefe et al. 2009
6. Anthropogenic Disturbances	Distance to Residential Cover	Select for sites closer to residential cover	O'Keefe et al. 2009
	Distance to roads	Select for sites closer to roads	O'Keefe et al. 2009
Subglobal Roost Characteristics	Combination Roost tree, Spanish moss density, roost tree DBH, distance to nearest taller tree, basal area, midstory stem density, and overstory stem density		
Subglobal Landscape Characteristics	Combination of landscape resources and anthropogenic disturbances		

Table 2. A priori models for northern yellow bat roost selection at three study areas in the Coastal Plain of South Carolina in summer (May-August) 2018 and 2019.

Model	Covariate	Prediction	Citation
1. Roost Structure Availability	Roost tree group	Select for <i>Quercus</i> spp. and Sabal Palmetto trees	Coleman et al. 2012, Castleberry et al. 2020
	Roost structure density	Select for higher Spanish moss and dead palm frond density	Menzel et al. 1999
2. Cover Type	Cover type	Select for maritime forest stands	Castleberry et al. 2020
3. Roost Protection and Permanence	Tree dominance	Select for subdominant trees	Coleman et al. 2012, Castleberry et al. 2020
	Canopy closure	Select for higher canopy closure	Castleberry et al. 2020
	Diameter at breast height	Select for higher DBH	Coleman et al. 2012, Menzel et al. 1999
4. Movement Ability	Midstory stem density	Select for lower stem density	Castleberry et al. 2020
	Overstory stem density	Select for lower overstory stem density	Coleman et al. 2012
	Overstory basal area	Select for higher overstory basal area	Castleberry et al. 2020
5. Landscape Characteristics	Distance to freshwater	Select trees closer to water	Castleberry et al. 2020
	Distance to salt marsh	Select trees closer to salt marsh	Castleberry et al. 2020
	Distance to edge	Select tree closer to hard edge	Castleberry et al. 2020
5. Anthropogenic Disturbances	Distance to road	Select for closer to roads	Perry et al. 2008
	Distance to residential cover	Select for closer to residential cover	Castleberry et al. 2020
Subglobal Roost Characteristics	Combination of tree group, roost structure density, roost tree DBH, dominance class, canopy closure, midstory stem density, basal area, and overstory stem density		
Subglobal Landscape Characteristics	Combination of landscape characteristics and anthropogenic disturbance		

Table 3. Mean and standard deviation of covariates for northern long-eared bat, tri-colored bat, and northern yellow bat roost and available trees in Bluffton SC, summer 2018 and 2019.

Covariate	Used		Available	
	Mean	SD	Mean	SD
Northern long-eared bat				
Tree Height (m)	19.9	1.7	20.8	6.3
Distance to Nearest Taller Tree	7.0	5.7	5.1	3.7
DBH (cm)	46.0	22.0	40.6	15.3
Canopy Closure (%)	90	5	83	10
Site Basal Area (m ²)	1.9	1.1	1.4	0.5
Overstory Stem Count (# of stems)	18.7	10.8	24.5	12.5
Midstory Stem Density (# of stems)	2.4	2.1	3.6	4.3
Distance to Freshwater (m)	512.3	238.4	717.1	758.4
Distance to Road (m)	127.4	133.3	180.8	102.0
Distance to Residential Cover (m)	1343.7	903.3	1890.2	1524.5
Proportion Forest within 165 m	0.98	0.03	0.91	0.10
Proportion Pine in surrounding plot	0.69	0.44	0.69	0.27
Proportion Oak in surrounding plot	0.18	0.30	0.12	0.14
Proportion Other in surrounding plot	0.13	0.19	0.19	0.27
Tri-colored bat				
Tree Height (m)	19.3	6.7	19.0	6.0
Distance to Nearest Taller Tree	5.8	3.5	5.9	2.7
DBH (cm)	52.4	21.3	40.4	15.3
Canopy Closure (%)	85	8	72	12
Site Basal Area (m ²)	1.8	0.7	1.2	0.6
Overstory Stem Count (# of stems)	14.4	8.2	15.8	9.4
Spanish moss Density (structure/m)	1.4	1.1	0.2	0.4
Midstory Stem Density (# of stems)	2.7	2.3	2.8	2.8
Distance to Freshwater (m)	475.9	243.9	511.9	409.0
Distance to Road (m)	135.2	94.0	189.1	197.5
Distance to Residential Cover (m)	766.4	507.9	843.5	809.8
Distance to Hard Edge (m)	89.5	63.9	75.5	80.3
Proportion Pine in surrounding plot	0.24	0.28	0.53	0.38
Proportion Oak in surrounding plot	0.43	0.33	0.24	0.28
Proportion Other in surrounding plot	0.33	0.22	0.23	0.31
Northern yellow bat				
Tree Height (m)	14.3	4.8	14.1	4.6
Distance to Nearest Taller Tree	5.5	3.1	3.9	2.4
DBH (cm)	44.8	25.1	34.0	16.6
Canopy Closure (%)	88	7	75	15
Site Basal Area (m ²)	1.79	0.60	1.48	0.61
Overstory Stem Count (# of stems)	17.7	7.7	19.1	9.1
Roost Structure Density (structure/m)	1.7	1.0	0.3	0.5

Midstory Stem Density (# of stems)	2.0	1.7	2.1	2.4
Distance to Freshwater (m)	282.3	230.8	365.5	276.6
Distance to Salt Marsh (m)	196.5	156.5	288.5	290.6
Distance to Road (m)	246.9	167.0	233.1	229.5
Distance to Residential Cover (m)	99.8	127.3	179.5	166.6
Distance to Hard Edge (m)	72.8	63.8	81.6	88.5
Proportion Pine in surrounding plot	0.34	0.28	0.53	0.26
Proportion Oak in surrounding plot	0.34	0.28	0.24	0.21
Proportion Sabal in surrounding plot	0.10	0.13	0.06	0.12
Proportion Other in surrounding plot	0.22	0.24	0.17	0.22

Table 4. Discrete choice models, number of parameters (K), model LogLikelihood, AIC_c , difference between model AIC_c and lowest AIC_c value (ΔAIC_c), model weight, and cumulative model weight of summer roost selection models for tri-colored bats (2019) and northern yellow bats (2018 and 2019) in Bluffton, SC.

Model	K	LogLikelihood	AIC_c	ΔAIC_c	Weight	Cumulative Weight
Tri-colored bat						
Roost Structure Availability	3	-10.50	27.80	0.00	0.94	0.94
Roost Characteristics Sub-global	8	-6.00	34.30	6.50	0.03	0.97
Roost Permanence	3	-13.90	34.70	6.90	0.03	1.00
Site Clutter	3	-24.00	54.90	27.10	0.00	1.00
Cover Type	2	-29.40	63.20	35.50	0.00	1.00
Anthropogenic Disturbance	2	-33.10	70.70	42.90	0.00	1.00
Landscape Resources	2	-34.80	74.10	46.30	0.00	1.00
Landscape Characteristics Sub-global	4	-32.90	75.20	47.50	0.00	1.00
Northern yellow bat						
Roost Structure Availability	3	-14.20	35.10	0.00	0.93	0.93
Roost Characteristics Sub-global	9	-7.90	40.40	5.30	0.06	0.99
Roost Permanence	3	-19.20	45.10	10.00	0.01	1.00
Site Clutter	3	-34.10	75.00	39.90	0.00	1.00
Anthropogenic Disturbance	2	-35.80	76.00	40.90	0.00	1.00
Landscape Characteristics Sub-global	5	-33.80	79.00	44.40	0.00	1.00
Landscape Resources	3	-36.90	80.60	45.50	0.00	1.00
Cover Type	2	-40.30	85.00	49.90	0.00	1.00

Table 5. Estimates, standard errors, and 85% confidence intervals for covariates in top models for tri-colored bat (2019) and northern yellow bat (2018 and 2019 summer roost selection in Bluffton, SC. Bold indicates important covariates given 85% confidence intervals that do not overlap zero.

Covariate	Estimate	SE	Lower CI	Upper CI
Tri-colored bat				
Pinus	-2.07	1.16	-3.74	-0.41
Quercus	-1.09	1.20	-2.82	0.65
Spanish Moss Density	2.52	0.86	1.28	3.77
Northern yellow bat				
Quercus	1.44	1.02	-0.03	2.91
Sabal	1.82	1.22	0.07	3.58
Roost Structure Density	2.11	0.55	1.32	2.91

FIGURES

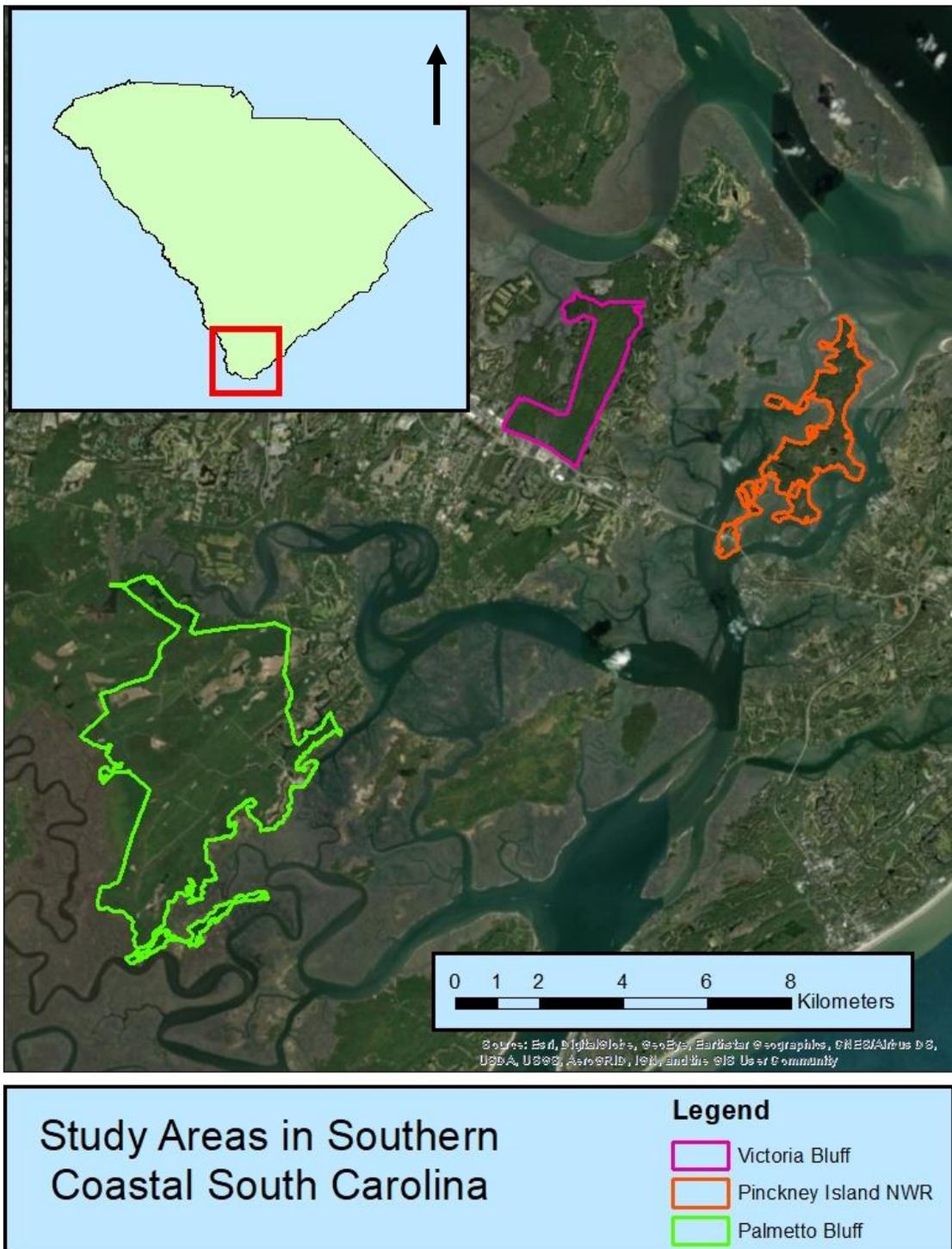


Figure 1. Study Areas in Bluffton, SC, USA.

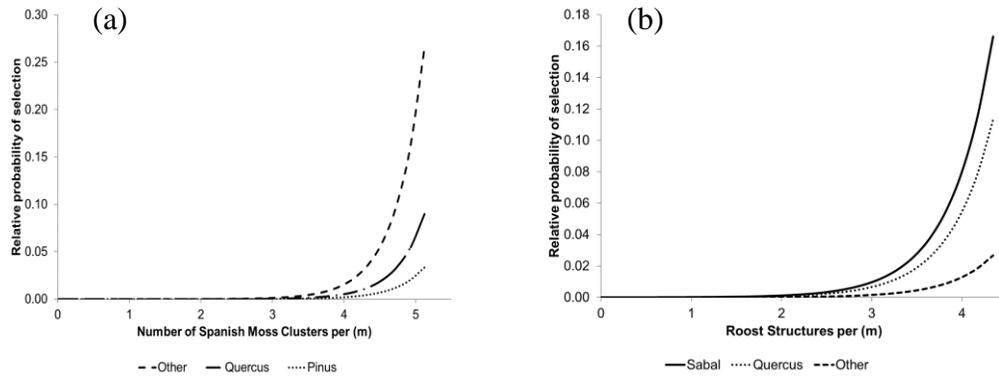


Figure 2. (a) Relative probability of summer roost selection for tri-colored bats based on Spanish moss density in *Quercus* spp., *Pinus* spp. and other trees, and for (b) northern yellow bats based on roost structure density in *Quercus* spp., *Sabal* spp. and other trees in coastal South Carolina, 2018 and 2019.

CHAPTER 2: NOCTURNAL HABITAT USE OF BAT SPECIES OF CONSERVATION CONCERN IN THE CHANGING LANDSCAPE OF COASTAL SOUTH CAROLINA

INTRODUCTION

Bats across the world rely on forests throughout various stages of their life. But, forests are threatened by human dominance over the landscape, particularly in terms of intensive logging, agriculture, and urbanization, which rank as some of the most urgent threats to bat conservation (Frick et al. 2019). Replacement of natural landcover by human land uses leaves a mosaic of fragmented habitat of varying quality (Bennett and Saunders 2010) and removes forest features that are used for nocturnal activity and foraging areas (Russo and Ancillotto 2014). Thus, forest loss, fragmentation, and degradation can negatively impact bats' ability to acquire resources, reproduce, and ultimately sustain populations.

During the nightly activity period, bats search for food, freshwater, and roosts. However, species use forests and landscapes differently based on their morphological and ecological traits. Small and maneuverable species exploit cluttered forests (areas with dense vegetation), large fast flying species exploit open areas, and some species exploit edges between forests and open areas (Aldridge and Rautenbach 1987). Thus, a diversity of forest structures is important so that many species' needs can be met. Other landscape features are also important for facilitating bat habitat use during nocturnal periods. Linear corridors including low-use forest roads and hard edges provide areas that some bats use for foraging and commuting (Morris et al. 2010; Amelon et al. 2014). Such features are especially important for large species that require open areas for foraging and movement

(Ford et al. 2006). Water features such as freshwater ponds and streams provide drinking water and abundant insects for foraging (Ford et al. 2006; Moore and Best 2018; Ancillotto et al. 2019). The loss or addition of forests, corridors, and freshwater sources can impact bat species' habitat use by causing changes in resource availability (Owen et al. 2003; Ethier and Fahrig 2011; Parker et al. 2019). Nightly habitat use also may vary by season when forest structure and resource availability shift. Research into bat habitat use typically occurs in summer (Loeb in review) and this precludes understanding of how bats use habitat across seasons (Weller et al. 2009). In the southeastern United States where winters are mild, bats can be active and forage during winter (Grider et al. 2016). However, seasonal changes in insect and vegetation communities may cause shifts in how bats use habitat.

The northern long-eared bat (*Myotis septentrionalis*), southeastern myotis (*M. austroriparius*), tri-colored bat (*Perimyotis subflavus*), and northern yellow bat (*Lasiurus intermedius*) are all species of conservation concern and year-round residents of the South Carolina Coastal Plain. Three of these species (the northern long-eared bat, southeastern myotis, and tri-colored bat) can be infected by the fungal pathogen associated with white nose syndrome (WNS). Northern long-eared bat populations have experienced steep declines throughout many parts of their range due to WNS and are federally listed as a threatened species. Northern long-eared bats were discovered in the Coastal Plain of South Carolina in 2016 and 2017 (White et al. 2018). These captures expanded the known range of the species which had only previously been documented in the upper Piedmont and Blue Ridge ecoregions of the state. During nocturnal activity

periods, this small and maneuverable species exploits interior forests where it can glean resting insects (Patriquin and Barclay 2003). The tri-colored bat, which uses edges along open habitat in its nocturnal activity period (Morris et al. 2010), has also experienced severe declines due to WNS in the upstate of South Carolina and is currently under review for protected status under the Endangered Species Act (USFWS 2017). The southeastern myotis is a highest priority threatened species in South Carolina, partially due to limited remaining habitat (Kindel 2017). Typical habitat for this species is swamp and bottomland forests (Menzel et al. 2005; Medlin and Risch 2008; Clement and Castleberry 2013) which are declining throughout the southeast. At least one southeastern myotis in Alabama was infected with WNS, however, populations do not yet seem to be greatly affected by the disease (USGS 2017) and habitat loss is likely the most critical conservation issue (BCI and SBDN 2013). While populations of these species may be impacted by WNS, the Outer Coastal Plain of South Carolina is a region devoid of caves and mines where conditions are amenable to the growth of the fungus. Thus, WNS likely does not pose a significant conservation threat in this region compared to others. The northern yellow bat is a species of special concern in South Carolina and while some limited research has been conducted on roosting ecology (Constantine 1958; Ivey 1959; Menzel et al. 1999; Hutchinson 2006; Coleman et al. 2012; Castleberry et al. 2020), no research on nocturnal habitat use has been conducted. The southeastern Atlantic and Gulf coasts are the only places in the United States where the northern yellow bat occurs. Mortalities have been documented at wind energy sites (Arnett and Baerwald 2013) and other anthropogenic structures such as towers (Crawford and Baker 1981), and while

such cases occur, they do not appear to be major causes of mortality. These species face a variety of conservation threats across their ranges. However, the greatest conservation threat in the Coastal Plain of South Carolina is likely habitat loss due to expanding anthropogenic land use.

Understanding seasonal habitat use for all of these species is necessary to inform conservation and management in this region where the predominate threat is habitat loss. Our objective was to determine habitat characteristics associated with nocturnal habitat use during summer and winter for *Myotis* spp., tri-colored bats, and northern yellow bats in coastal South Carolina. We hypothesized that habitat use would vary based on morphology of the species or species group as well as by season for some species (Norberg and Rayner 1987). Specifically, we predicted that in summer *Myotis* spp. would use interior forest sites while tri-colored bats and northern yellow bats would use non-forested sites and sites associated with hard edges (Ford et al. 2006; Morris et al. 2010; Jantzen and Fenton 2013). We predicted that all species or groups would use sites in close proximity to landscape features such as freshwater, roads for commuting, and nearby potential foraging areas. Additionally, we predicted that *Myotis* spp. would use sites surrounded by a high proportion of forest, while tri-colored bats and northern yellow bats would use sites surrounded by low proportions of forest (Ivey 1959; Ford et al. 2006; Starbuck et al. 2015). We also predicted that *Myotis* spp. would use study areas that were predominately forested while tri-colored bats and northern yellow bats would use study areas with low amounts of forest (Morris et al. 2010; Starbuck et al. 2015). Finally, we predicted that *Myotis* spp. and northern yellow bats would use sites far from human

disturbance, while tri-colored bats would use sites close to human disturbance (Johnson et al. 2008; Starbuck et al. 2015; Rodríguez-Aguilar et al. 2017). In addition, we hypothesized that habitat use by some species would vary across seasons due to changing forest structure and resource availability. Specifically, we predicted that there would be no difference in habitat use between seasons for *Myotis* spp. but that tri-colored bats and northern yellow bats would shift from using open sites to using forested sites and to upland and bottomland forest habitat types during winter (Burles et al. 2009).

METHODS

Study Area

This study took place at three areas in Beaufort County (32.35 , -80.69) in the southern Coastal Plain of South Carolina: Palmetto Bluff, Pickney Island National Wildlife Refuge, and Victoria Bluff Heritage Preserve (See Figure 1, Chapter 1). All three study areas are located within the southeastern climate region (Karl and Koss 1984). Average temperature during the winter (December-March) is 11.8°C and average total precipitation is 33 cm; average temperature during the summer survey period (May-August) is 26.2°C with an average total precipitation of 52 cm (20-year average; NOAA 2020). Habitat types in all three study areas included upland forests (pine savannahs, mixed hardwood-pine forests, and maritime forests), bottomland forests, ponds, maintained fields, and salt marshes. Palmetto Bluff is a 5,165 ha multi-use property that consisted of low-density housing, areas that were zoned for future development of suburban housing, and 132 ha under conservation protection or easement which cannot be developed. The areas we surveyed at Palmetto Bluff were made up of approximately

96% upland forest, 1% bottomland forest, < 1% fields, < 1% ponds, 2% residential cover, and had about 42 km of salt marsh edge. Pinckney Island is an approximately 1,640 ha National Wildlife Refuge. Pinckney Island was made up of approximately 87% upland forest, 4% bottomland forest, 7% fields, 2% ponds, and had about 33 km of salt marsh edge. Victoria Bluff is an approximately 470 ha state-owned heritage preserve surrounded by suburban development. Victoria Bluff was made up of approximately 74% upland forest, 23% bottomland forest, 3% fields, and had approximately 4 km of salt marsh edge; no freshwater ponds were on this property. Neither Pinckney Island nor Victoria Bluff contained significant urban cover on their property, but both were bordered by varying degrees of residential or high intensity urban development.

Acoustic Sampling

We used Anabat Express acoustic detectors (Titley Scientific, Columbia, MO) to record bat passes February through March 2018, December 2018 through March 2019, and May through August 2018 and 2019 on Palmetto Bluff, Victoria Bluff, and Pinckney Island National Wildlife Refuge. We stratified our sampling among five habitat types: upland forest, bottomland forest, open field, along salt marsh edges, and freshwater ponds. We used ArcMap (version 10.5.1, ESRI, Redlands, CA) to create tessellation grids over all study areas where each cell was 0.4 ha to allow for flexibility of detector placement. We removed cells that contained > 1 habitat type or hard edges to reduce the likelihood that we were recording bats using a different habitat type than that associated with the cell. From the remaining grid we selected cells based on a Generalized Random Tessellation Stratified (GRTS) sampling design using R package “Spsurvey”. We

restricted salt marsh cells to those that had one edge touching land in order to assure access to a site and to avoid loss of detectors due to high tide. As ponds are discrete landscape features, they were not included in the GRTS sampling framework. Instead, we assigned each pond a number, randomly ordered them, and selected the first 25 ponds to survey. We surveyed 25 sites (cells where detectors were placed) within each habitat type over both summers for a total of 125 sites across all habitat types during the study. In winter we surveyed 121 of these same 125 sites; we were not able to survey four sites at Palmetto Bluff because of time constraints. In winter we surveyed 24 sites in bottomland forest, 23 in fields, 25 at ponds, 25 in salt marsh, and 24 in upland forests. We surveyed 81 sites at Palmetto Bluff (77 in winter), 30 at Pinckney Island, and 14 at Victoria Bluff.

During summer, we surveyed sites for four nights and during winter we surveyed sites for 5-10 nights to account for potentially lower activity related to lower temperatures (Grider et al. 2016). During both seasons acoustic recording began 30 minutes before sunset and ended 30 minutes after sunrise. Detectors were set to a data division ratio of 8 and a sensitivity of 115. We placed acoustic units on 3.5 m high poles as close to the center of sample cells as possible (within forests always ≥ 25 m away from the nearest edge), in locations that would maximize ability to record bats (lower clutter areas). We also faced microphones in the direction with the least amount of vegetative clutter. For field and salt marsh sites we faced detectors toward open areas and away from edges. For pond sites, we strategically selected locations where detectors could face toward the pond without being blocked by the dense vegetation that surrounded many ponds. We did not avoid placement of units during rain or storm events. Storms during

summer were typically scattered across the landscape and did not last for extended periods of time. Even though detectors may have been out during inclement weather (rain, low temperatures), the effects of rain and temperature on bat activity were accounted for in our models.

At each site, we characterized the vegetation structure surrounding the detector by creating a 0.05 ha circular plot (radius = 12.5 m) around each detector. We confirmed habitat type from the GIS layer (upland forest, bottomland forest, field, pond, and salt marsh) and estimated basal area using a variable plot method and angle gauge with a Basal Area Factor (BAF) of 10. Additionally, we measured canopy closure at the plot center and 6 m from the center in each cardinal direction using a spherical densiometer (Model-A, Forest Densiometers, Forestry Suppliers Inc., Jackson, MS). All five measurements were averaged to obtain a canopy closure value for the plot. To characterize midstory stem density, we created a transect through the plot center along a randomly selected bearing and counted all stems ≥ 4 cm diameter at breast height (DBH) and < 10 cm DBH within 1 m of either side of the transect. We determined the location of each plot center with a GeoExplorer 2008 Series Global Positioning System unit (Trimble Inc., Sunnyvale, CA). We used ArcMap to calculate distance to forest edge, distance to residential cover, distance to roads, distance to freshwater, distance to nearest hardwood stand, distance to nearest pine stand, and percent forest cover within a 250 m buffer for the northern yellow bat and a 200 m buffer for the *Myotis* spp. and tri-colored bat. We chose these buffers based on the foraging ranges of northern long-eared bats and scale of response or foraging ranges of other bats with similar ecology and morphology to tri-

colored bats and northern yellow bats (Broders et al. 2006; Moretto et al. 2019). We obtained weather data from the Beaufort Merritt Field Airport Weather Station (32.4806, -80.7192, Elevation: 11.3 m) in Beaufort, SC using the R package “riem” and calculated average nighttime temperature and total rainfall.

Analysis

We used Anlook (Version 4.2n 2017) and two custom filters to remove recorded call files containing only background noise and non-search phase calls such as feeding buzzes and social calls. The first filter removed files containing only background noise and low frequency interference, and the remaining files were used as an estimate of overall bat activity. The second filter removed passes that were low quality or had < 4 pulses. We identified filtered passes using Kaleidoscope Pro (Version 4.2.0) and vetted all passes for correct identification. We grouped northern long-eared bat and southeastern myotis, big brown bats (*Eptesicus fuscus*) and silver haired bats (*Lasionycteris noctivagans*), and red bats (*Lasiurus borealis*) and Seminole bats (*L. seminolus*) due to similarities in their call structures. We then developed nightly detection histories for *Myotis* spp., tri-colored bats, and northern yellow bats for each site and season for each species.

We used Program R version 3.6.1 (R Core Team 2019) to conduct occupancy analyses for each species in package “unmarked”. First, we modeled detection probability of each species or species group using models based on weather, site clutter, and date (Table 1) while using the global model for occupancy (MacKenzie et al. 2018). Second, we identified top models using a $\Delta AIC_c \leq 4$ and retained important detection covariates

from out top models as defined by 85% confidence intervals that did not overlap zero (Arnold 2010), and modeled simple single season occupancy for each species or species group. We scaled all continuous covariates prior to analysis and screened for correlation. We found evidence of correlation ($|r| > 0.60$) between canopy closure and basal area and therefore did not include them in the same models for northern long-eared and tri-colored bats and did not include canopy closure in any models for the northern yellow bat because of differing species biology.

For each species or species group we developed additive models for occupancy based on multiple competing hypotheses that varied by species or species groups due to differences in morphological characteristics and how those relate to space use (Norberg and Rayner 1987). We hypothesized that habitat use by *Myotis* spp., tri-colored bats, and northern yellow bats would be influenced by habitat type, forest structure, site vegetative clutter, access to landscape features, access to commuting features, and anthropogenic disturbance (Table 2; Table 3; Table 4). We also included a null model for all species and a global model for *Myotis* spp. For the tri-colored bat and northern yellow bat analyses we used subglobal models that did not include habitat type because the global models were overparameterized and did not converge. For each species or species group we tested model fit of the most parameterized detection and occupancy model (MacKenzie and Bailey 2004) in package “AICcmodavg” with 1000 simulations. If the global model did not converge, we used the most parameterized model possible. We ranked models using Akaike’s Information Criterion corrected for small sample size (AIC_c) or Quasi Akaike’s Information Criterion corrected for small sample size ($QAIC_c$) when goodness

of fit tests indicated overdispersion. We used adjusted standard errors (SE times $\sqrt{\hat{c}}$) when there was evidence of overdispersion. We defined the confidence set of top models as those with $\Delta AIC_c \leq 4$ and obtained model-averaged estimates using R package “AICcmodavg” when there was uncertainty among models containing the same covariates. If models in the confidence set contained no common covariates, we present all models that were in the confidence set with their weights and interpreted each model separately. Additionally, we determined that individual covariates were important for both detection and occupancy if their 85% confidence intervals did not overlap zero (Arnold 2010). Foraging bats are highly mobile and therefore can cause a violation of the assumption of site closure by not constantly occupying a site. While we used occupancy modeling, it is important to note that given the violation of this assumption, our results should be interpreted as habitat use (Mackenzie 2005).

RESULTS

During summer 2018 and 2019 we surveyed for 500 detector nights and recorded 61,928 echolocation passes. After filtering out poor quality passes, we identified 25,248 passes to eight species or species groups. Of the identified passes, 32% (8,038) were tri-colored bats, 26% (6,595) were red bats or Seminole bats, 15% (4,009) were evening bats (*Nycticeius humeralis*), 11% (2,969) were big brown bats or silver haired bats, 10% (2,652) were Brazilian free-tailed bats (*Tadarida brasiliensis*), 3% (825) were northern yellow bats, 1% (116) were *Myotis* spp., and 1% (44) were hoary bats (*Lasiurus cinereus*).

During winter 2018 and 2019 we surveyed for 885 detector nights and recorded 52,651 bat passes. After removing poor quality passes, we identified 18,356 passes to eight species or species groups. Of the identified passes, 25% (4,627) were Brazilian free-tailed bats, 22% (3,995) were tri-colored bats, 18% (3,327) were red bats or Seminole bats, 18% (3,206) were big brown bats or silver haired bats, 8% (1,448) were evening bats, 4% (788) were hoary bats, 4% (729) were northern yellow bats, and 1% (236) were *Myotis* spp.

***Myotis* spp.**

We detected *Myotis* spp. at 42 sites (34%) during summer. We did not find evidence of overdispersion in our data ($\hat{c} = 0.73$, $P = 0.76$). Five models were in the detection probability confidence set (rain, null, temperature, full weather, and clutter models; Table 5), but midstory stem density was the only important covariate so we retained it in the occupancy models (Appendix 1). The landscape model was the only one in the confidence set for occupancy and had a weight of 0.94 (Table 6). Important covariates in this model were distance to water and distance to hardwood stands (Table 7). Occupancy decreased with increasing distance to hardwood dominated stands (Figure 1a) and distance to water (Figure 1b).

We detected *Myotis* spp. at 46 sites (38%) during winter. We found no evidence for overdispersion in our data ($\hat{c} = 1.32$, $P = 0.06$) so we used AIC_c to rank both detection and occupancy models. Five detection models were in the confidence set (temperature model, which was the top model, null model, rain model, full weather model, and date model; Table 5). Important covariates in this model were temperature and date, so these

were retained in the occupancy model (Appendix 1). The landscape resources model was the only one in the confidence set for occupancy and had a weight of 0.95 (Table 6).

Important covariates were distance to water, distance to pine stand, and distance to hardwood stand (Table 7). Occupancy decreased with increasing distance to hardwood stand (Figure 1c), distance to freshwater (Figure 1d), and distance to pine stand (Figure 1e).

Tri-colored bats

We detected tri-colored bats at 106 sites (85%) during summer. The data were overdispersed ($\hat{c} = 3.17$, $P = 0.001$) so we used QAIC_c to rank both detection and occupancy models. Five detection models (null model, temperature model, rain model, full weather model, and date model) were in the confidence set (Table 5) indicating high uncertainty. Temperature was important so it was retained in the occupancy models (Appendix 1). The null occupancy model was the only model in the confidence set indicating that no covariates that we measured were good predictors of occupancy (Table 6).

We detected tri-colored bats at 78 sites (64%) during winter. We did not find evidence of overdispersion in our data ($\hat{c} = 1.18$, $P = 0.12$) so we used AIC_c to rank the detection and occupancy models. The global model was the only one in the confidence set for detection models (Table 5). Temperature, rain, basal area, and date were all important detection covariates (Appendix 1), so we retained them in the occupancy model. The habitat type model was the only one in the confidence set for occupancy with a weight of 0.99 (Table 6), and salt marsh and upland forest were important. Occupancy

was lower in salt marsh and upland forest sites than in bottomland forest (Table 7, Figure 2a). Occupancy in field and pond sites was not different from occupancy in bottomland forest sites.

Northern yellow bats

We detected northern yellow bats at 71 sites (57%) during summer. We found evidence of overdispersion in our data ($\hat{c} = 1.86$, $P = 0.03$) so we used QAIC_c to rank detection and occupancy models. The null, temperature, rain, full weather, and date models were all within the confidence set (Table 5), but no covariates were important likely due to the null model being the top model (Appendix 1). We retained a null detection model for our occupancy models. The habitat type and global models were both in the confidence set for occupancy (Table 6). Habitat types field, pond, and salt marsh, as well as distance to water and distance to salt marsh were all important covariates (Table 7). Occupancy was higher at field sites, pond sites, and salt marsh sites than at bottomland forest sites (Figure 2b). Occupancy in upland forest sites was not different from occupancy in bottomland forest sites (Figure 2b). Occupancy was also higher closer to water and closer to salt marsh (Figure 3a, 3b).

We detected northern yellow bats at 48 sites (40%) during winter. We did not find evidence of overdispersion in our data ($\hat{c} = 1.14$, $P = 0.268$), so we used AIC_c to rank our models of detection and occupancy. The only model in our confidence set was the global model, with a weight of 0.99 (Table 5). Important covariates were rain, basal area, and temperature, which we retained in our occupancy models (Appendix 1). Two models were within the confidence set of occupancy models, habitat type with a weight of 0.63

and landscape resources with a weight of 0.35 (Table 6). Salt marsh and upland forest habitat types were important as were proportion of forest within 250 m, distance to water, and distance to salt marsh (Table 7). Occupancy was lower at salt marsh and upland forest sites compared to bottomland forest sites (Figure 2c) and higher closer to freshwater and salt marsh (Figure 3c, 3d). Occupancy was also higher in areas with a higher proportion of forest within 250 m (Figure 3e).

DISCUSSION

We observed support for our hypotheses that nocturnal habitat use by the three focal species or species group of our study would vary based on morphology and ecology, and that these characteristics would result in shifts in habitat use between summer and winter. During summer, habitat use was related to characteristics that we would expect based on how morphologically distinct bats interact with their environment. The large fast flying northern yellow bat used open areas and the more maneuverable *Myotis* spp. were associated with forests. However, when resource availability and forest structure likely changed with season, we saw that northern yellow bats and tri-colored bats used interior forest habitat that we may not expect if we simply considered their morphology along with summer forest conditions and insect abundance. Our results highlight that changes in habitat use occur between seasons and that failure to account for different ecological needs throughout the year may limit our understanding of important habitat features (Weller et al. 2009).

Although *Myotis* spp. habitat use was not associated with any site characteristics that we measured, the landscape surrounding sites was important and as we predicted, use

did not change between summer and winter. Distance to hardwood stands and distance to freshwater were important during both seasons, as well as distance to pine stands during winter. Greater probability of use in proximity to forested stands reflects myotis habitat use elsewhere, where they use sites within a variety of forests and sites with high proportions of surrounding forest (Patriquin and Barclay 2003; Ford et al. 2006; Morris et al. 2010; Starbuck et al. 2015). Hardwood stands at our study areas included bottomland hardwood and maritime forests which provide complex structure from which *Myotis* species can glean insects (Ford et al. 2006). Southeastern myotis are also closely tied to bottomland forests for roosting, using basal cavities in trees such as water tupelo (*Nyssa aquatica*), black tupelo (*N. sylvatica*), and sweetgum (*Liquidambar styraciflua*) (Clement and Castleberry 2013; Fleming et al. 2013) which dominated bottomland forests in our study area. Northern long-eared bats use a diversity of hardwood and pine trees across their range for roosting (Silvis et al. 2016). Like other species, *Myotis spp.* in our study may use foraging habitat close to roost sites to reduce energy used for commuting (Veilleux et al. 2004; Broders et al. 2006).

It is possible that some of our results on *Myotis spp.* were impacted by grouping the two species, and we may not have picked up on how habitat use varied between these species. For example, northern long-eared bats in Kentucky forage closer to pine stands than hardwood stands (Lacki et al. 2009) in summer, whereas southeastern myotis in South Carolina use pine stands less than hardwood stands (Ford et al. 2006). Thus, the importance of proximity to pine stands in winter may reflect northern long-eared bat habitat use more than southeastern myotis habitat use. Nevertheless, the foraging strategy

of both species allows individuals to take advantage of structurally complex forests where they can glean resting insects, a behavior especially important in facilitating foraging during cool periods (Burles et al. 2009).

We found that tri-colored bat habitat use in summer was distributed across most of the landscape counter to what we predicted. However, in winter we saw use shift to bottomland forests, ponds, and fields more than salt marsh and upland forest habitat types which partially reflected our predictions. While some studies have reported that tri-colored bat habitat use is associated with edges, high canopy closure, and low vegetation density (Ford et al. 2006; Loeb and O’Keefe 2006; Morris et al. 2010), others have found that use does not differ among open canopy, closed canopy, harvested, and unharvested forests (Menzel et al. 2002). The presence of tri-colored bats across 85% of our sites may explain why we had difficulty in explaining variation in occupancy among sites and indicates that tri-colored bats display generalist behavior during summer in our study area. This generalist behavior may more broadly reflect why there is variation among other studies as well. In contrast to summer, habitat use in winter was higher in bottomland forests, ponds, and fields than in salt marsh and upland forest, potentially reflecting changes in resource availability between seasons. Although insect abundance does not affect bat activity during summer in Coastal South Carolina (Moore and Best 2018), it is possible that there is a threshold of low availability below which habitat use is constrained to areas where insects are more available. When temperatures decrease, insects are not able to sustain flight for prolonged periods of time (Rowley and Graham 1968). Bottomland forests may therefore provide not only structure for insects to rest on

but water sources, potentially supporting a higher abundance of insects in wet forests than dry ones (Janzen and Schoener 1968). Finally, fields and ponds had similar use to bottomland forests and likely also provide resources for tri-colored bats. Freshwater and forest edges may provide places to forage and drink even when resources are more limited in winter (Morris et al. 2010; Stahlschmidt et al. 2012).

As we predicted, summer habitat use by northern yellow bats was associated with the three open habitat types (salt marsh, fields, and ponds) more than with forested habitats. However, in winter, use shifted to bottomland forests, fields, and ponds more than salt marsh and upland forests. The summer associations with open habitat types supported our prediction that forests are too cluttered for efficient foraging by this relatively large species (Norberg and Rayner 1987; Morris et al. 2010). Northern yellow bats were also more likely to use sites closer to salt marsh, providing further support that this is an important habitat for this species in summer. However, northern yellow bat habitat use shifted between summer and winter. During winter, habitat use was lower in salt marsh and upland forest compared to bottomland forests but similar among bottomland forests, fields, and ponds. Shifts in insect communities away from the more open salt marsh where there is little resting space or protection from the elements (Verboom and Huitema 1997) may explain low use of this habitat type by northern yellow bats in winter compared to summer. Nonetheless, use was still high at sites close to salt marsh during winter even though use of this habitat was low. On average, summer roost sites were closer to salt marsh than random sites (see Chapter 1). Thus, it is possible

that northern yellow bats use areas close to salt marsh in winter because individual core home ranges remain constant throughout the year.

Northern yellow bats used bottomland forests in the winter, but not in the summer. While bottomland forests were mostly dominated by deciduous hardwoods like *Nyssa* spp., upland forests were mostly dominated by evergreen species including live oak and pines. Canopy closure decreased by about 30% on average in bottomland forests during winter but only decreased by about 11% in upland forests. The greater reduction in clutter in bottomland forests may open flight space for this and other species, making these sites easier to maneuver and forage in (Brigham et al. 1997; Loeb and O'Keefe 2006; Suarez-Rubio et al. 2018). Although use of fields was not different from use of bottomland forests in winter for the northern yellow bat, we saw a decrease in probability of use from summer to winter and use of fields was greater than use of salt marsh (Figure 2b, 2c). These changes in use may reflect relative changes in insect abundance. In winter, insect abundance may be higher in fields than in the salt marsh because fields were typically surrounded by more hard edge than salt marshes in our study area. Such edges are positively related to insect density as they provide more protection than open areas (Verboom and Huitema 1997).

Our data suggest that freshwater ponds and bottomland forests were important for multiple species. During summer and winter, northern yellow bat and *Myotis* spp. were more likely to use sites that were closer to freshwater, and during winter tri-colored bat habitat use was high at ponds. Ponds are important for many bats, especially in human dominated areas (Henderson and Broders 2008; Fabianek et al. 2011; Ancillotto et al.

2019; Parker et al. 2019). Human constructed ponds provided most of the freshwater sources in our study areas and such retention ponds provided permanent water sources to bats. Permanent water sources are particularly important on coastal islands where freshwater can be scarce. In addition to ponds, our data suggest that bottomland forests were important for multiple species. The tri-colored bat and northern yellow bat used bottomland forests more than other habitat types and *Myotis* spp. used sites close to hardwood stands, many of which were bottomland forests. Our results provide further support of the importance of bottomland forests to bats in this region (Grider et al. 2016). The importance of these forests is particularly noteworthy in our study area because of the small percentage of land they make up compared to other forest types.

We predicted that distance to residential development would influence habitat use of all species studied, but the model containing this covariate did not receive support in any of our analyses. Disturbance and fragmentation associated with low-density housing development in our study areas may have increased complementation (i.e., access to multiple habitats and resources needed at various times of day) (Dunning et al. 1992). Complementation can increase bat activity by providing access to both roosting and foraging sites (Ethier and Fahrig 2011) and intermediate disturbance due to low-level development may increase access to a diversity of resources (Gehrt and Chelvig 2004; Rhodes and Catterall 2008; Threlfall et al. 2011). However, bat occupancy is negatively impacted by even low-level urban development in Australia (Caryl et al. 2016), though this study looked at a broader spatial scale than ours. At a similar broad spatial scale, for

example across the Coastal Plain of South Carolina, habitat use may be impacted by urbanization because of more variable degrees of habitat loss and human disturbance.

We used occupancy modeling to analyze our data which allowed us to account for imperfect detection. While occupancy modeling is a useful tool for understanding habitat associations it has some drawbacks. Levels of activity (i.e., number of passes recorded) may show different patterns of habitat use than site occupancy because sites with low and high activity have the same weight in occupancy analyses. Additionally, abundance and occupancy can be misleading when they do not reflect habitat quality because intraspecific competition can push individuals to suboptimal habitat or habitat sinks (Horne 1983). However, even with these drawbacks and when standard occupancy model assumptions like site closure are violated, such models are still appropriate to estimate habitat use (Mackenzie 2005). Another important consideration in using occupancy models is that information about availability of resources is not considered. For example, acoustic studies may provide data on sites that are used by species, but cannot be used to provide information on habitat selection or preference (Miller et al. 2003). While acoustic studies may draw similar conclusions to use and selection studies using telemetry, they do not always provide the same habitat association results at various orders of selection (Morris et al. 2011). Studying resource selection of individuals instead of use helps to elucidate complex relationships relating to habitat quality and preference. Nonetheless, habitat use provides information about important resources and changes over time to help inform management about habitat associations.

Collectively, our results suggest that as the Coastal Plain of South Carolina continues to go through rapid forest loss, retention of important features including ponds, bottomland forests, hardwood forests, pine dominated forests, and coastal salt marshes would help meet the needs of a diversity of bat species during different times of the year. The variation we observed in habitat use among species supports the hypothesis that morphologically different bats use habitat structures differently. Additionally, changes in resources and vegetation throughout the year resulted in changes in habitat use. Had our research been only focused on the summer reproductive period, we may have drawn conclusions about habitat use that diminished the importance of bottomland forests for some species. While increasing low-level disturbance and adding features like freshwater retention ponds may benefit bats, it also has the potential to remove critical forest resources. The loss of forest features, even for bat species that do not predominately use them or use them only during one season may lead to unexpected consequences to populations in this region. As loss of forests continues, retention of natural forest patches and important landscape features will help meet the diversity of needs for many species.

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TABLES

Table 1. A priori models (1-7) for detection of target bat species during Summer and Winter 2018 and 2019 in coastal South Carolina (+ indicates positive effect of covariate on detection, - indicates a negative effect of covariate on detection).

Model	Covariates	Summer Prediction	Winter Prediction
1. Temperature	Temperature	+	+
2. Rain	Rain	-	-
3. Full Weather	Temperature	+	+
	Rain	-	-
4. Clutter	Midstory Stem Density	-	-
	Overstory Basal Area	-	-
5. Date	Date ²	+	-
6. Null			
7. Global			

Table 2. A priori models (1-8) for *Myotis* bat nocturnal habitat use and predictions for summer and winter (+ indicates positive effect of covariate on occupancy, - indicates a negative effect of covariate on occupancy).

Models	Covariates	Summer Predictions	Winter Predictions	Citation
1. Interior Forest	Canopy Closure ²	+	+	Lacki et al. 2009
2. Habitat type	Habitat Type: Forested Wetland	+	+	Jantzen and Fenton 2013
	Habitat Type: Field and Wildlife Foodplot	-	-	Jantzen and Fenton 2013
	Habitat Type: Pond	-	-	Henderson and Broders 2008, Moore and Best 2018
	Habitat Type: Salt Marsh	-	-	Jantzen and Fenton 2013
	Habitat Type: Upland Forest	+	+	Jantzen and Fenton 2013
	3. Site Clutter	Basal Area	+	+
Midstory Stem Density		-	-	Loeb and O'Keefe 2006
4. Landscape Commuting	Distance to Edge	-	-	Patriquin and Barclay 2003, Jantzen and Fenton 2013
	Distance to Road	-	-	Pauli et al. 2017
5. Landscape Resources	Distance to Water	-	-	Henderson and Borders 2008
	Distance to Pine Stand	-	-	Lacki et al. 2009, Confortin and Brown 2018
	Distance to Hardwood Stands	-	-	Ford et al. 2006
	Proportion of Forest in 200 m Buffer	+	+	Starbuck et al. 2015, Broders et al. 2006
6. Anthropogenic Disturbance	Distance to Residential Cover	+	+	Johnson et al. 2008
	Distance to Road	+	+	Pauli et al. 2017
	Study Area: Palmetto Bluff	+	+	Starbuck et al. 2015
	Study Area: Victoria Bluff	+	+	Starbuck et al. 2015
	Study Area: Pinckney Island	-	-	Starbuck et al. 2015
7. Null				
8. Global				

Table 3. A priori models (1-8) for tri-colored bat nocturnal habitat use and predictions for summer and winter (+ indicates positive effect of covariate on occupancy, - indicates a negative effect of covariate on occupancy).

Models	Covariate	Summer Prediction	Winter Prediction	Citation
1. Edge and Interior Forests	Canopy Closure ²	+	+	Ford et al. 2006
	Distance to Edge	-	-	Morris et al. 2010
2. Site Clutter	Midstory Stem Density	-	-	Ford et al. 2006, Loeb and O'Keefe 2006
3. Landscape Commuting	Basal Area	-	+	Ford et al. 2006
	Distance to Edge	-	-	Morris et al. 2010
	Proportion of Forest in 200 m	-	-	Starbuck et al. 2015
4. Landscape Resources	Distance to Road	-	-	Morris et al. 2010
	Distance to Water	-	-	Ford et al. 2006
	Distance to Hardwood Stands	-	-	Perry et al. 2007
	Distance to Edge	-	-	Morris et al. 2010
5. Anthropogenic Disturbance	Proportion of Forest in 200 m	-	-	Starbuck et al. 2015, Broders et al. 2006
	Distance to Road	-	-	Morris et al. 2010
6. Habitat Type	Study Area: Palmetto Bluff	+	+	Starbuck et al. 2015
	Study Area: Victoria Bluff	+	+	Starbuck et al. 2015
	Study Area: Pinckney Island	-	-	Starbuck et al. 2015
	Distance to Edge	-	-	Morris et al. 2010
	Distance to Residential Area	-	-	Starbuck et al. 2015
	Habitat Type: Bottomland Forest	-	+	Ford et al. 2006
	Habitat Type: Field and Wildlife Food Plot	+	-	Ford et al. 2006
	Habitat Type: Pond	+	+	Fabianek et al. 2011
Habitat Type: Salt Marsh	+	-	Ford et al. 2006	
	Habitat Type: Upland Forest	-	+	Ford et al. 2006
7. Null				
8. SubGlobal				

Table 4. A priori models (1-8) for northern yellow bat nocturnal habitat use and predictions for summer and winter (+ indicates positive effect of covariate on occupancy, - indicates a negative effect of covariate on occupancy).

Model	Covariate	Summer Predictions	Winter Predictions	Citation
1. Habitat Type	Habitat Type: Bottomland Forest	-	+	Morris et al. 2010
	Habitat Type: Field	+	-	Morris et al. 2010
	Habitat Type: Pond	+	+	Morris et al. 2010
	Habitat Type: Salt Marsh	+	-	Morris et al. 2010
	Habitat Type: Upland Forest	-	+	Morris et al. 2010, Norberg
2. Site Clutter	Basal Area	-	+	Patriquin and Barclay 2003
	Midstory	-	-	Patriquin and Barclay 2003
3. Landscape Resources	Proportion of Forest in 250 m	-	+	Ivey 1959
	Distance to Water	-	-	Webster et al. 1980
	Distance to Salt Marsh	-	+	Ivey 1959
4. Landscape Commuting	Proportion of Forest in 250 m	-	+	Ivey 1959, Moretto et al. 2019
	Distance to Road	-	-	Amelon et al. 2014
	Distance to Salt Marsh	-	+	Ivey 1959
5. Human Disturbance	Distance to Road	-	-	Amelon et al. 2014
	Distance to Residential Cover	+	+	Rodriguez-Aguilar et al. 2016
6. Study Area	Study Area: Palmetto Bluff	+	+	Morris et al. 2010
	Study Area: Pinckney Island	+	-	Morris et al. 2010
	Study Area: Victoria Bluff	-	+	Morris et al. 2010
7. Null				
8. SubGlobal				

Table 5. Confidence sets ($\Delta AICc$ or $\Delta QAICc < 4$) of detection models for *Myotis* spp., tri-colored bats, and northern yellow bats in summer and winter 2018 and 2019, in Bluffton, SC. Quasi Akaike Information Criterion is used for model sets denoted by *

Models	K	Q/AICc	$\Delta Q/AICc$	Model Likelihood	Q/AICc Weight	Quasi/Log Likelihood	Cumulative Weight
<i>Myotis</i>							
Summer							
Rain	16	380.85	0.00	1.00	0.38	-171.91	0.38
Null	15	381.22	0.37	0.83	0.31	-173.41	0.69
Temperature	16	383.39	2.54	0.28	0.11	-173.18	0.79
Full Weather	17	383.50	2.65	0.27	0.10	-171.89	0.89
Clutter	17	384.28	3.42	0.18	0.07	-172.28	0.96
Winter							
Temperature	16	562.12	0.00	1.00	0.45	-262.45	0.45
Full Weather	17	563.31	1.19	0.55	0.25	-261.68	0.70
Null	15	565.00	2.88	0.24	0.11	-265.22	0.81
Date	17	565.75	3.62	0.16	0.07	-262.90	0.89
Clutter	17	566.12	4.00	0.14	0.06	-263.09	0.95
Tri-colored bat							
Summer*							
Null	15	176.22	0.00	1.00	0.35	-70.91	0.35
Temperature	16	176.28	0.06	0.97	0.34	-69.62	0.69
Rain	16	178.23	2.01	0.36	0.13	-70.60	0.82
Full Weather	17	178.85	2.63	0.27	0.09	-69.56	0.91
Date	17	179.93	3.71	0.16	0.05	-70.10	0.97
Winter							
Global	16	868.37	0.00	1.00	0.69	-415.57	0.69
Full weather	12	870.50	2.13	0.34	0.24	-421.80	0.93
Northern yellow bat							
Summer*							
Null	14	280.53	0.00	1.00	0.43	-124.36	0.43
Temperature	15	281.49	0.95	0.62	0.27	-123.54	0.70
Rain	15	282.99	2.46	0.29	0.13	-124.29	0.82
Full Weather	16	284.12	3.59	0.17	0.07	-123.54	0.89
Date	16	284.44	3.91	0.14	0.06	-123.70	0.96
Winter							
Global	15	548.58	0.00	1.00	0.99	-256.98	1.00

Table 6. Confidence sets ($\Delta AICc$ or $\Delta QAICc < 4$) for occupancy models of *Myotis* bats, tri-colored bats, and northern yellow bats in summer and winter 2018 and 2019, in Bluffton, SC. Quasi Akaike Information Criterion is used for model sets denoted by *

Models	K	Q/AICc	$\Delta Q/AICc$	Model Likelihood	Q/AICcWeight	Log Likelihood	Cumulative Weight
<i>Myotis</i>							
Summer							
Landscape Resources	7	363.97	0.00	1.00	0.94	-174.51	0.94
Winter							
Landscape Resources	9	556.18	0.00	1.00	0.95	-268.28	0.95
Tri-colored bats							
Summer*							
Null	4	151.74	0.00	1.00	0.76	-71.71	0.76
Winter							
Habitat Type	11	853.92	0.00	1.00	0.99	-414.75	0.99
Northern yellow bats							
Summer*							
Habitat Type	7	277.23	0.00	1.00	0.83	-131.14	0.83
Global	14	280.53	3.30	0.19	0.16	-124.36	0.99
Winter							
Habitat Type	9	535.91	0.00	1.00	0.63	-258.14	0.63
Landscape Resources	8	537.06	1.15	0.56	0.35	-259.89	0.98

Table 7. Estimates, standard errors, and 85% confidence intervals for covariates in top models for *Myotis* spp., tri-colored bat, and northern yellow bat occupancy in summer and winter 2018 and 2019 in Bluffton, SC (bold indicates important covariates)

	Estimate	SE	Lower CI	Upper CI
Myotis				
Summer				
Intercept	-0.36	0.31	-0.81	0.09
Distance to Water	-0.45	0.28	-0.85	-0.04
Distance to Pine	-0.49	0.37	-1.02	0.04
Proportion of Forest	0.43	0.32	-0.02	0.88
Distance to Hardwood	-0.60	0.34	-1.09	-0.10
Winter				
Intercept	-0.66	0.31	-1.11	-0.21
Distance to Water	-1.08	0.35	-1.58	-0.57
Distance to Pine Stand	-1.01	0.44	-1.64	-0.38
Proportion of Forest	0.33	0.29	-0.10	0.75
Distance to Hardwood Stand	-0.56	0.34	-1.04	-0.07
Tri-colored bats				
Summer				
Intercept	1.74	0.14	1.53	1.95
Winter				
Intercept	2.68	1.07	1.14	4.22
Habitat type: Field	-1.70	1.22	-3.46	0.06
Habitat Type: Pond	5.56	18.96	-21.74	32.86
Habitat Type: Salt Marsh	-3.00	1.15	-4.66	-1.34
Habitat Type: Upland Forest	-1.96	1.15	-3.62	-0.30
Northern yellow bats				
Summer				
Intercept	-1.63	0.85	-2.85	-0.40
Habitat Type: Field	3.76	1.50	1.60	5.91
Habitat Type: Pond	3.80	1.52	1.61	6.00
Habitat Type: Salt Marsh	3.19	1.37	1.22	5.17
Habitat Type: Upland Forest	0.00	1.14	-1.64	1.65
Basal Area	0.06	0.75	-1.01	1.14
Midstory Stem Density	0.35	0.41	-0.24	0.94
Proportion of Forest	-0.82	0.73	-1.87	0.23
Distance to Road	0.25	0.58	-0.58	1.08
Distance to Water	-1.66	0.75	-2.74	-0.58
Distance to Residential Area	0.84	0.66	-0.12	1.79
Distance to Salt Marsh	-1.08	0.53	-1.85	-0.31

Winter

Intercept	1.76	1.63	-0.59	4.10
Habitat Type: Field	-1.74	1.70	-4.18	0.71
Habitat Type: Pond	0.36	1.85	-2.31	3.02
Habitat Type: Salt Marsh	-3.57	1.74	-6.08	-1.06
Habitat Type: Upland Forest	-3.10	1.67	-5.50	-0.69
Intercept	-0.16	0.29	-0.58	0.25
Proportion of Forest	0.45	0.28	0.04	0.86
Distance to Water	-1.48	0.37	-2.01	-0.95
Distance to Salt Marsh	-0.45	0.26	-0.82	-0.08

FIGURES

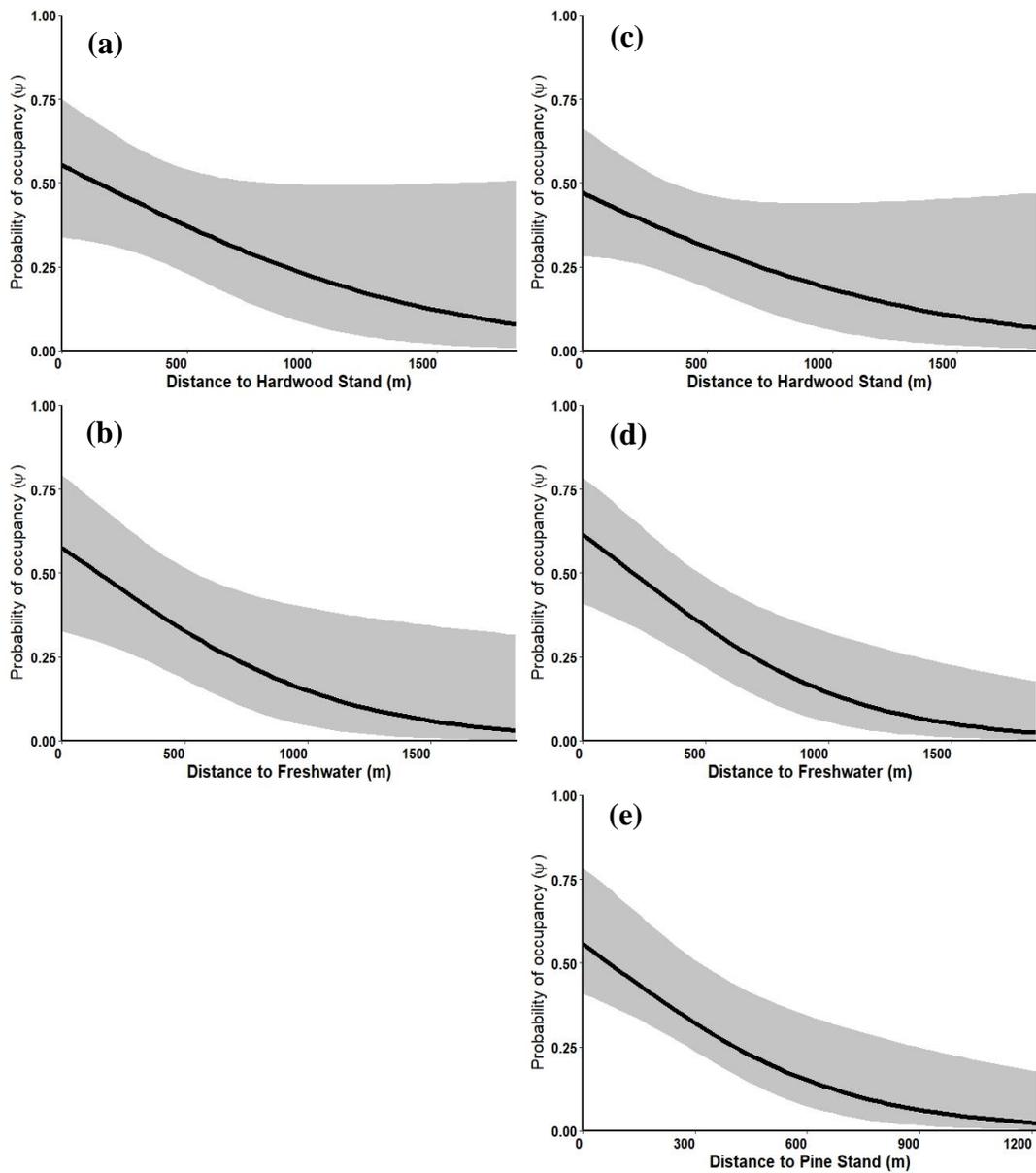


Figure 1. Probability of *Myotis* spp. occupancy in summer based on (a) distance to hardwood stand, and (b) distance to freshwater, and in winter based on (c) distance to hardwood stand, (d) distance to freshwater, and (e) distance to pine stand in Bluffton, SC, 2018 and 2019.

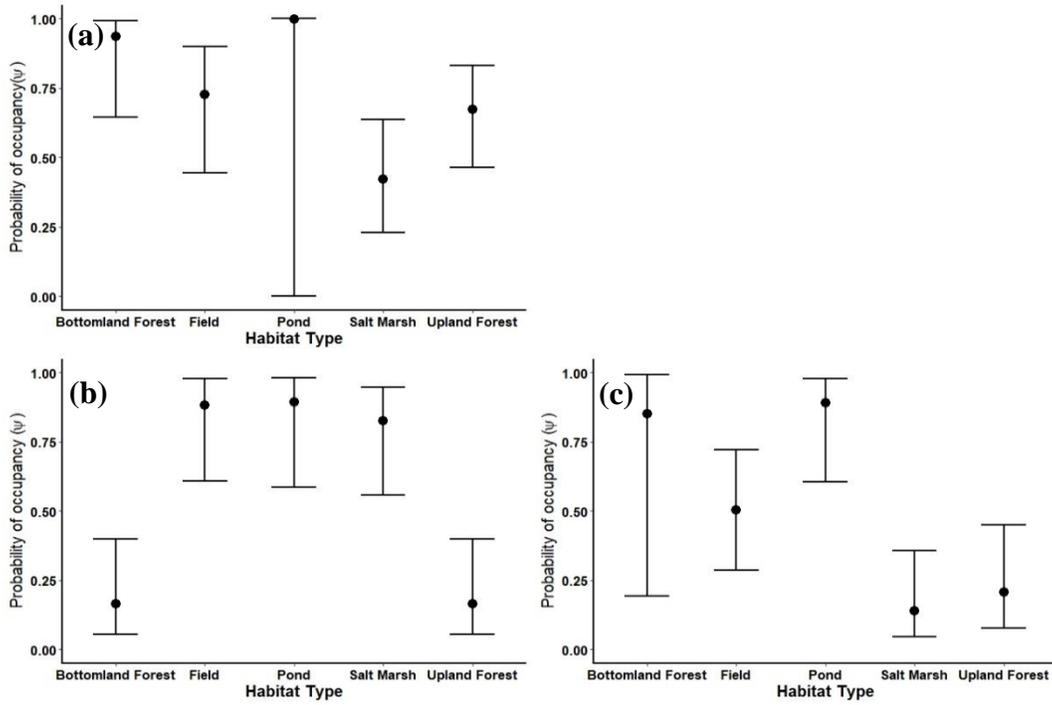


Figure 2. Probability of site occupancy based on habitat type (reference category: bottomland forest) of (a) tri-colored bats in winter, (b) northern yellow bats in summer and, (c) northern yellow bats in winter in Bluffton, SC, 2018 and 2019.

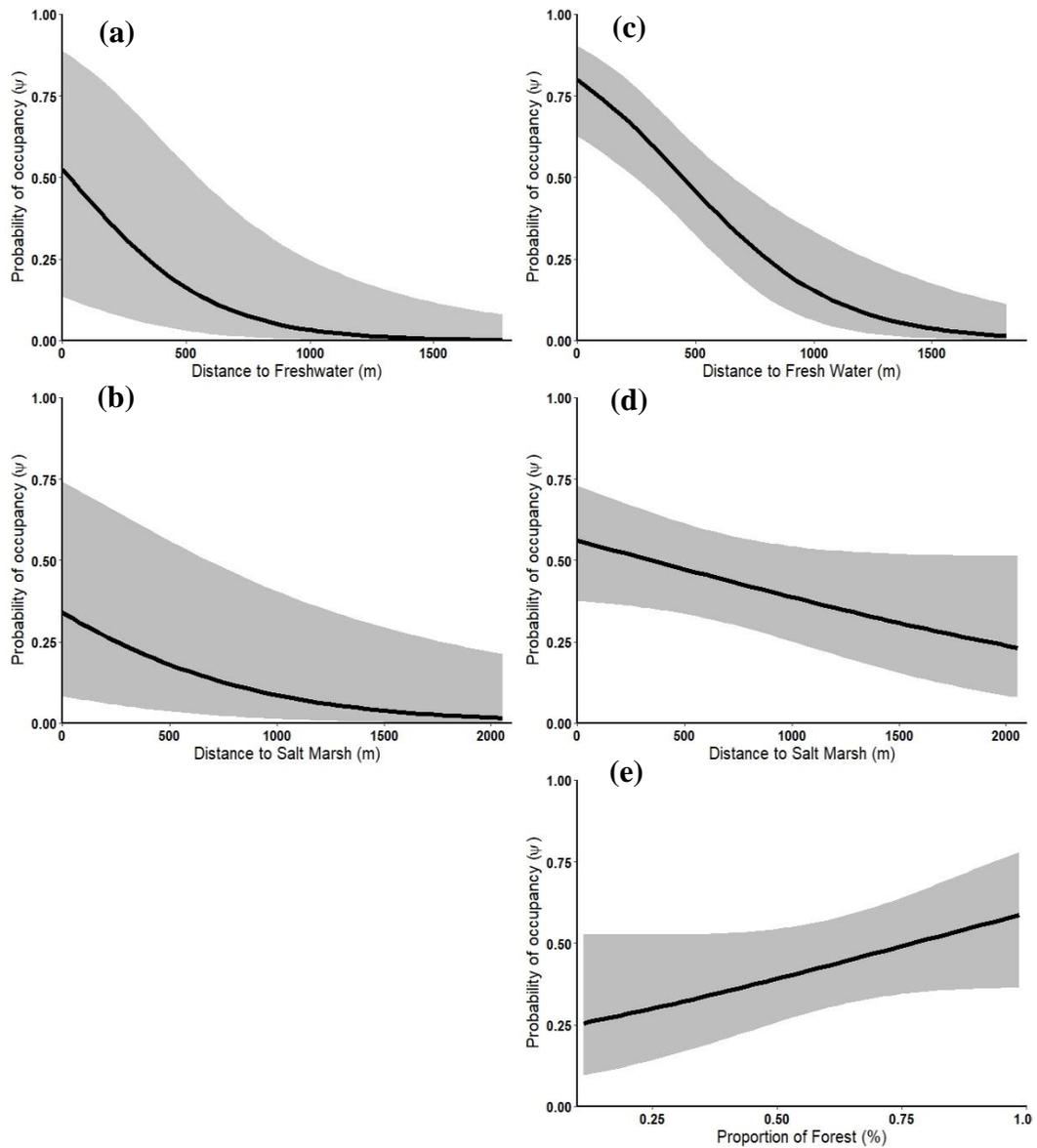


Figure 3. Probability of Northern yellow bat site occupancy in summer based on (a) distance to freshwater and (b) distance to salt marsh and in winter based on (c) distance to freshwater, (d) distance to salt marsh, and (e) proportion of forest within 250m buffer in Bluffton, SC, 2018 and 2019.

APPENDIX

Table 1. Estimates, standard errors, and 85% confidence intervals for covariates in top models of *Myotis* spp., tri-colored bat, and northern yellow bat detection probability in summer and winter 2018 and 2019 in Bluffton, SC (bold indicates important covariates).

	Estimate	SE	Lower CI	Upper CI
Myotis				
Summer				
Intercept	-0.87	0.24	-1.21	-0.52
Rain	-0.46	0.36	-0.98	0.06
Temp	0.07	0.17	-0.17	0.32
Basal Area	-0.10	0.29	-0.51	0.31
Midstory	0.33	0.19	0.05	0.61
Winter				
Intercept	-1.02	17.00	-1.24	-0.81
Temp	0.32	0.13	0.14	0.50
Rain	-0.14	0.13	-0.33	0.05
Date	0.56	0.28	0.16	0.95
Date²	-0.09	0.05	-0.15	-0.02
Tri-colored bats				
Summer				
Intercept	1.75	0.26	1.38	2.13
Temp	0.39	0.26	0.02	0.76
Rain	-0.12	0.20	-0.42	0.17
Date	0.24	0.29	-0.18	0.66
Date ²	0.23	0.28	-0.17	0.64
Winter				
Intercept	-0.52	0.10	-0.67	-0.38
Temp	0.99	0.11	0.83	1.15
Rain	-0.18	0.08	-0.29	-0.07
Basal Area	-0.22	0.09	-0.35	-0.08
Midstory Stem Density	0.08	0.08	-0.03	0.20
Date	0.65	0.25	0.29	1.01
Date²	-0.12	0.04	-0.18	-0.06
Northern yellow bats				
Summer				
Intercept	0.32	0.18	0.06	0.58
Temp	0.23	0.18	-0.03	0.49
Rain	-0.05	0.22	-0.36	0.27
Date	-0.24	0.22	-0.55	0.07
Date ²	0.06	0.13	-0.12	0.24
Winter				

Intercept	-1.22	0.16	-1.44	-0.99
Rain	-0.35	0.15	-0.56	-0.13
Basal Area	-0.81	0.19	-1.09	-0.53
Midstory	0.00	0.12	-0.18	0.17
Temp	1.01	0.15	0.79	1.22
Date	0.02	0.32	-0.44	0.49
Date ²	-0.03	0.05	-0.11	0.04
