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Roosting Ecology of Northern Long-eared Bats in Coastal South Carolina

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Abstract - *Myotis septentrionalis* (Northern Long-eared Bat) has experienced severe population declines due to the impacts of white-nose syndrome, although some populations along the Atlantic Coast appear to be persisting. Our objectives were to document the presence of Northern Long-eared Bats across the Coastal Plain of South Carolina and describe roost characteristics and other aspects of the bats' ecology. We captured 45 Northern Long-eared Bats from April to August 2017–2024 across 4 sites. We radio-tagged 30 bats and tracked them to 99 day roosts. Almost all (92.9%) roosts were in pines, predominantly *Pinus taeda* (Loblolly Pine) and *P. palustris* (Longleaf Pine); 78.8% of roost trees were alive, although adult females were more likely than males to use snags. Fifty-four percent of roosts were in stands burned within the past 4 years. Our results suggest that pine forests are important for Northern Long-eared Bats in coastal South Carolina and that prescribed fire is compatible with Northern Long-eared Bat management.

Introduction

Summer roosting ecology of North American bats has received considerable study over the past 3 decades (Clerc et al. 2021). Much has been learned about the types of structures used for roosting, including the landscapes and forest types containing those structures, particularly in eastern North America (Drake et al. 2020). Although general patterns have begun to emerge (Kalcounis-Rüeppell et al. 2005), many species exhibit considerable variation in roosting ecology across their ranges (e.g., Garcia et al. 2023, O'Keefe and Loeb 2017). Thus, managing roosting habitat at a particular location or within a region may require knowledge of species' requirements at the local or regional scale.

Myotis septentrionalis (Trouessart) (Northern Long-eared Bat) is listed as endangered in the USA and Canada, primarily due to the effects of white-nose syndrome (WNS), a lethal fungal disease (COSEWIC 2013, Federal Register 2022). Populations of the Northern Long-eared Bat have declined up to 99% across 79% of its range (Cheng et al. 2021), which extends from the east coast of North America to Manitoba and south to Louisiana (Silvis et al. 2016). Many studies suggest there is considerable variation in the roosting ecology of this species across the range (Clerc et al. 2021, Drake et al. 2020). For example, Northern Long-eared Bats have been documented roosting in at least 49 tree species and select for either hardwoods or pines, depending on the study (Garcia et al. 2023, Silvis et al. 2016). These bats frequently switch roosts and primarily use crevices or cavities in snags, although they use live trees as well (e.g., Andersen and Geluso 2022, Carter and Feldhamer 2005, Foster and Kurta 1999, Timpone et al. 2010). Despite being considered a forest interior species, they have also been found in urban or suburban areas (Burrell and Bergeson 2022, Thorne et al. 2021).

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Northern Long-eared Bats were not believed to inhabit the Atlantic Coastal Plain south of the Great Dismal Swamp in Virginia until 2007, when individuals were captured along roadways next to mature forest stands in northeastern North Carolina (Morris et al. 2009). Both adults and juveniles were captured, indicating a reproducing population. Subsequently, they have been captured throughout much of the Coastal Plain of North Carolina (Jordan 2020) and in southeastern South Carolina (Shute 2020, White et al. 2018). In the Coastal Plain, typical cave or mine hibernation sites for Northern Long-eared Bats are not widely available. For example, only 2 caves are known in the Coastal Plains of North Carolina and only 1 cave is known in the Upper Coastal Plain of South Carolina. None of these caves contain Northern Long-eared Bats, although 1 cave in North Carolina is sometimes used by *Perimyotis subflavus* (Cuvier) (Tricolored Bat) and the cave in South Carolina is used by *M. austroriparius* (Rhoads) (Southeastern Myotis). Instead, Northern Long-eared Bats in coastal North Carolina use tree cavities and crevices as winter roosts (Jordan 2020). Further, bats in the Southeast often feed and drink during winter (Bernard et al. 2021, Whitaker et al. 1997), and Northern Long-eared Bats are active throughout much of the winter in these areas (Grider et al. 2016, Jordan 2020). Their high activity levels in winter, ability to feed, and use of trees instead of cold, humid caves where they enter deep hibernation, may help to decrease susceptibility to WNS. Thus, the Coastal Plains of the Carolinas may represent a refugium from the disease, similar to coastal islands in the Northeast where bats are active for longer periods of time before entering hibernation in artificial structures (Hoff et al. 2024).

Given the potential importance of coastal areas for the long-term persistence of Northern Long-eared Bats in eastern North America, our goal was to learn more about the spring and summer roosting ecology of Northern Long-eared Bats in coastal South Carolina. Our specific objectives were to document the presence of Northern Long-eared Bats across the Coastal Plain of South Carolina and describe their roosts and roosting habitats, as well as their reproductive phenology during spring and summer. We were specifically interested in determining tree species and forest types used for roosting, as well as the potential effects of management, particularly prescribed fire, on habitat use. We also wanted to determine how consistent Northern Long-eared Bat roosting behaviors were across sites and between sexes.

Field-site Description

We report on Northern Long-eared Bats captured and tracked from April through August 2017–2024 at 4 sites spanning much of the South Carolina coast (Fig. 1): Francis Marion National Forest (FMNF), Palmetto Bluff (PB), Santee Coastal Reserve Wildlife Management Area (SCR WMA), and Waccamaw National Wildlife Refuge (WNWR). The FMNF in Berkeley and Charleston counties contains 105,066 ha; the PB in Beaufort County, 8093 ha; the SCR WMA in Charleston County, 9712 ha; and the WNWR in Georgetown County, 23,419 ha, although Northern Long-eared Bats were only captured on Sandy Island (3709 ha) within the WNWR. All sites contain a mixture of upland pine forests, primarily *Pinus palustris* Mill. (Longleaf Pine) and *P. taeda* L. (Loblolly Pine), upland hardwood forests, mixed pine-hardwood forests, bottomland hardwood forests, forested and non-forested wetlands, and freshwater ponds. Additional habitat types include Carolina Bay wetlands at the FMNF and the SCR WMA, and golf courses, maintained fields, maritime forest, and suburban development at PB. Management consisted primarily of prescribed fire, maintenance of early successional habitat, and timber harvesting, although the intensity and levels of these activities varied across sites. The climate in coastal South Carolina is humid subtropical, with average lows ranging from 14.4°C in April to 24.4°C in August, and average highs from

23.3°C in April to 31.7°C in July (https://weatherspark.com/countries/US/SC). Rainfall can occur throughout the summer, with monthly averages ranging from 66 to 130 mm.

Methods

Capture and radio-tracking

Capture and radio-tracking of bats were conducted by separate groups of researchers at each site using similar methods. Bats were captured with 2.5–12-m-wide single-, double-, and triple-high mist-nets set across or parallel to flyways (e.g., roads, trails, wetlands, ponds, and streams). Nets were opened near dusk and closed 4–5 h later, weather permitting. We recorded species, sex, age (adult or juvenile, based on ossification of the metacarpal-phalangeal joint of the fourth phalanges; Brunet-Rossinni and Wilkinson 2009), reproductive condition (non-reproductive, pregnant, lactating, or post-lactating; Racey 2009), body mass, forearm length, and habitat type (e.g., pine or hardwood forest, wetland, bottomland, riparian zone) of the capture location. We placed a 2.9-mm aluminum lipped band (Porzana Limited,

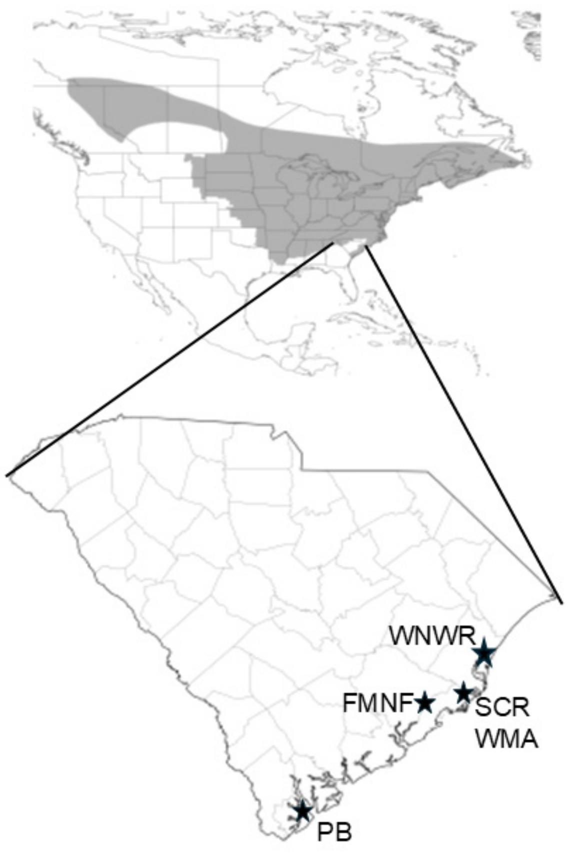

Figure 1. Map of study sites surveyed for Northern Long-eared Bats in coastal South Carolina at Waccamaw National Wildlife Refuge (WNWR), Santee Coastal Reserve and Wildlife Management Area (SCR WMA), Francis Marion National Forest (FMNF), and Palmetto Bluff (PB), April–August 2017–2024. Shaded area in top map represents the range of the Northern Long-eared Bat.

East Sussex, United Kingdom) on the forearm of some bats. We placed a 0.22–0.31-g radio-transmitter (LB-2X or BD-2X, Holohil Systems Ltd, Carp, ON, Canada) on the dorsum of Northern Long-eared Bats by trimming the fur on the back and attaching the transmitter with surgical glue (Perma-Type Company, Inc., Plainville, CT; Osto-Bond, Montreal Ostomy, QC, Canada; or Torbot Skin Bonding Cement, Warwick, RI). All transmitters weighed <5% of bats' body mass (Aldridge and Brigham 1988). Methods were approved by the U.S. Forest Service Institutional Animal Care and Use Committee (IACUC Protocol #2019-009) and Clemson University IACUC (#2017-072) and followed the guidelines of the American Society of Mammalogists for the capture and handling of bats (Sikes 2016).

On the day following tagging and during subsequent days, we attempted to locate bats using a receiver (TRX-2000, Wildlife Materials, Murphysboro, IL; Advanced Telemetry Systems, Isanti, MN; or Lotek Biotracker, New Market, ON, Canada) and 3-, 4-, or 5-element antennae (Wildlife Materials, or Lotek Biotracker). Emergence counts were done when possible. When a roost was located, we collected the following data: tree species, diameter at breast height (DBH), tree height, roost type (e.g., cavity, exfoliating bark if determined via visual confirmation of the bat in the roost or at emergence), decomposition state of tree (live, live-damaged, or dead), and GPS location. We plotted roost tree coordinates in ArcGIS Pro (Version 3.3.1) and overlayed them with various data layers in the LandFire database (Rollins 2009), to determine forest type and percent canopy cover within a 30-m grid cell of the roost tree. We ground-truthed the LandFire roost stand classifications, based on field observations. For analysis, we combined bottomland hardwoods and pocosins as "Bottomlands", and pine and pine flatwoods as "Pine". We obtained spatial data layers concerning prescribed fire history from fire managers at FMNF, SCR WMA, and WNWR, and recorded whether each roost was within a stand that burned within the past 5 years, and the time since the last burn. For each bat, we used ArcGIS to measure the distance from the capture site to each roost, and distance between roosts.

Data analyses

Data were analyzed in R version 4.4.0 (R Core Team 2024). One bat at PB was captured and tracked in 4 separate years. For the purposes of our analyses, we treated this bat as a unique individual each year when we examined the number of days tracked, trees used per bat, and days per roost. We used χ^2 tests of independence in the crosstable package (Chaltiel 2025) to determine whether relative use of tree species groups (hardwood or pine), decomposition state, roost types, roost stand forest types, and prescribed fire status (burned or not burned within past 5 years) differed among sites and between adult males and females. We only included adults when examining sex differences because juveniles, depending on their age, may or may not have been following their mothers. We used the psych package (Revelle 2025) to obtain descriptive statistics of continuous variables. Due to small sample sizes of roosts at some sites and non-normal data distributions, we used the Brown-Mood Median Test to assess differences in the number of trees used per bat, number of days per roost, distance between capture sites and roosts, distances among roosts, DBH, tree height, and canopy cover among sites and between sexes using the coin package (Hothorn et al. 2006). When statistical differences were detected among sites, we used post-hoc tests in the rcompanion package (Mangiafico 2025) to determine which sites varied from others. Unless stated otherwise, all data are reported as the mean ± standard deviation (SD), and we used $\alpha \leq 0.05$ to denote statistical significance.

Results

We captured 45 Northern Long-eared Bats across the 4 sites (20 at FMNF, 6 at PB, 17 at SCR WMA, and 2 at WNWR). We caught 13 adult females, 25 adult males, 4 juvenile females, and 3 juvenile males. All but 2 adult females were in reproductive condition, with 5 pregnant, 2 lactating, and 4 post-lactating. Pregnant females were captured from 27 April through 22 May; lactating females, 29 May through 18 June; and post-lactating females 26 June through 26 July. Only 1 of the 32 banded bats was recaptured. This was an adult male captured at PB in July 2018 and recaptured and radio-tagged in May 2019, July 2021, and July 2024. When recaptured in 2019, the band appeared fine with no abrasions or injuries seen. However, when this bat was recaptured in 2021, the band had moved to his humerus. The original band was removed and replaced with another that also moved to the humerus by 2024. The second band was not removed because it was too tight; however, the wing membrane was not punctured, and the bat appeared otherwise to be in good condition. At FMNF, PB, and WNWR, Northern Long-eared Bats were captured most often in pine or mixed pine-hardwood stands, whereas at SCR WMA, bats were primarily captured in bottomland hardwood and riparian habitats (Fig. 2).

All Northern Long-eared Bats—except 4 at SCR WMA and 1 at PB—were radio-tagged. We located roosts for 30 bats (9 adult females, 15 adult males, 4 juvenile females, and 2 juvenile males) in 99 trees (58 at FMNF, 12 at PB, 25 at SCR WMA, and 4 at WNWR). Bats were tracked for 4.0 ± 2.0 days (range 1–8), and they used 3.1 ± 1.7 trees (range 1–7). Adult females used 3.7 ± 1.9 trees (median = 4) over the tracking period, whereas males used 2.6 ± 1.3 trees (median = 2.5), although this was not statistically different ($z = 1.70$, $P = 0.09$). Bats stayed in roosts for 1.3 ± 0.9 days (range = 1–6), and the number of days per roost did not

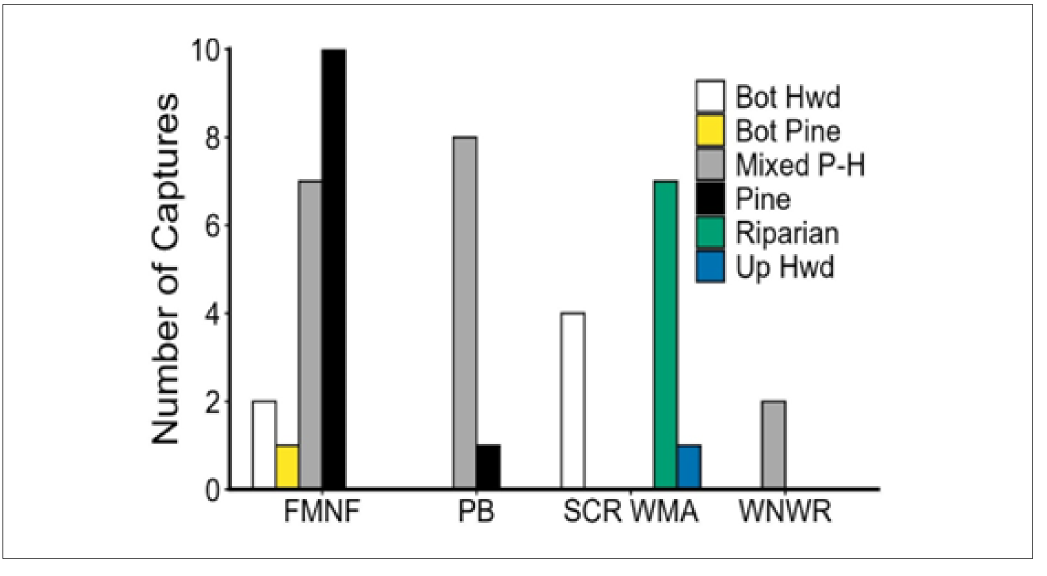

Figure 2. Forest types of Northern Long-eared Bat capture sites at Francis Marion National Forest (FMNF), Palmetto Bluff (PB), South Carolina Reserve and Wildlife Management Area (SCR WMA), and Waccamaw National Wildlife Refuge (WNWR), in South Carolina, April–August 2017–2024. Bot Hwd = bottomland hardwood; Bot Pine = bottomland pine; Mixed P-H = mixed pine–hardwood; and Up Hwd = upland hardwood forests.

differ between adult males and females (z = -1.68, $P = 0.10$). The number of bats emerging from a roost ranged from 1 to 12. All adult males roosted individually, whereas adult females and juveniles either roosted alone or with a presumed maternity colony.

The distance between capture sites and each bat's roost was 930 ± 841 m (median = 707 m, range = 120–4260 m), and these distances varied among sites ($\chi^2 = 27.96$, df = 3, $P < 0.0001$). Distance between capture sites and roosts was lower at FMNF than at PB ($P = 0.04$) and at SCR WMA ($P < 0.0001$) (Fig. 3A). The roosts of 2 bats at SCR WMA were considerably farther (3718–4260 m) from their capture sites than most other bats at SCR WMA and other sites (<1900 m). Even with these 2 bats removed from the dataset, distances between capture and roost sites were greater at SCR WMA than FMNF ($P = 0.0007$). Although females tended to roost farther from their capture site (1234 ± 1219 km, median = 820, range = 155–4260 m) than males (740 ± 611 m, median = 567 m, range = 120–3,719 m), this difference was not significant (z = 1.29, $P = 0.20$). The distance between roosts was 279 ± 394 m (median = 135 m, range 2–2164 m) and did not vary by site ($\chi^2 = 3.21$, df = 3, $P = 0.36$). Most roosts were within 500 m of each other, although some bats moved much greater

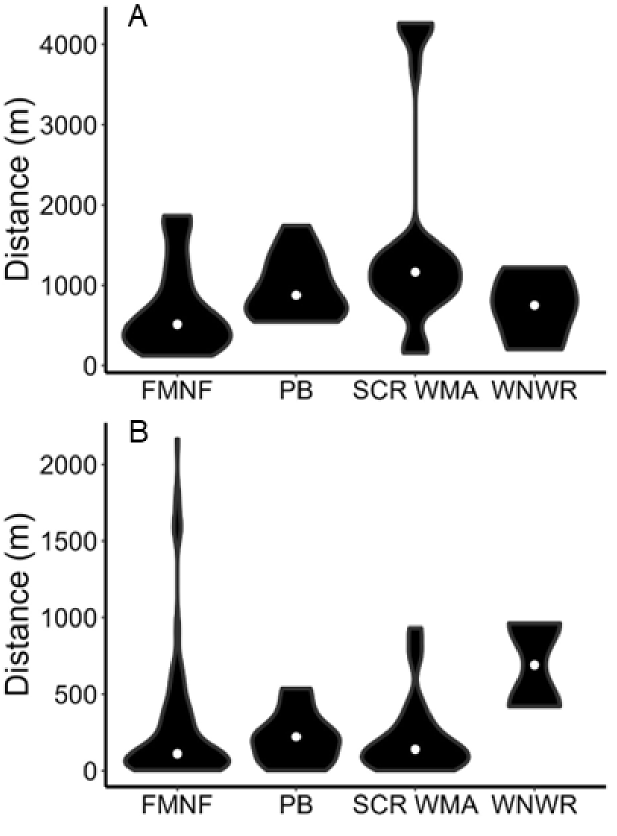

Figure 3. Violin plots of A) distance between capture sites and roosts, and B) distance between roosts for Northern Long-eared Bats at Francis Marion National Forest (FMNF), Palmetto Bluff (PB), Santee Coastal Reserve Wildlife Management Area (SCR WMA), and Waccamaw National Wildlife Refuge (WNWR), in South Carolina, April–August 2017–2024.

distances (Fig. 3B). Distance between roosts of males (346 ± 453 m, median = 220 m, range = 3–2164 m) was greater (z = -3.80, P = 0.0001) than between roosts of females (239 ± 426 m, median = 64 m, range = 4–1604 m).

Most roost trees (92.9%) were pines, including 1 *P. echinata* Mill. (Shortleaf Pine), 6 *P. elliottii* Engelm. (Slash Pine), 50 Longleaf Pine, and 35 Loblolly Pine. We also located roosts in 1 *Acer rubrum* L. (Red Maple), 1 *Liquidambar styraciflua* L. (Sweetgum), 1 *Nyssa aquatica* L. (Water Tupelo), 2 *N. sylvatica* Marshall (Black Gum), and 2 *Quercus falcata* Michx. (Southern Red Oak). The propensity to use pines was consistent across sites (χ^2 = 2.34, df = 3, P = 0.51) and between adult males and females (χ^2 = 1.18, df = 1, P = 0.28; Fig. 4A–B). Use of hardwoods was slightly greater at PB; however, this was driven by 1 individual that used 2 Black Gums. Most roost trees (78.8%) were alive, while 3.0% were

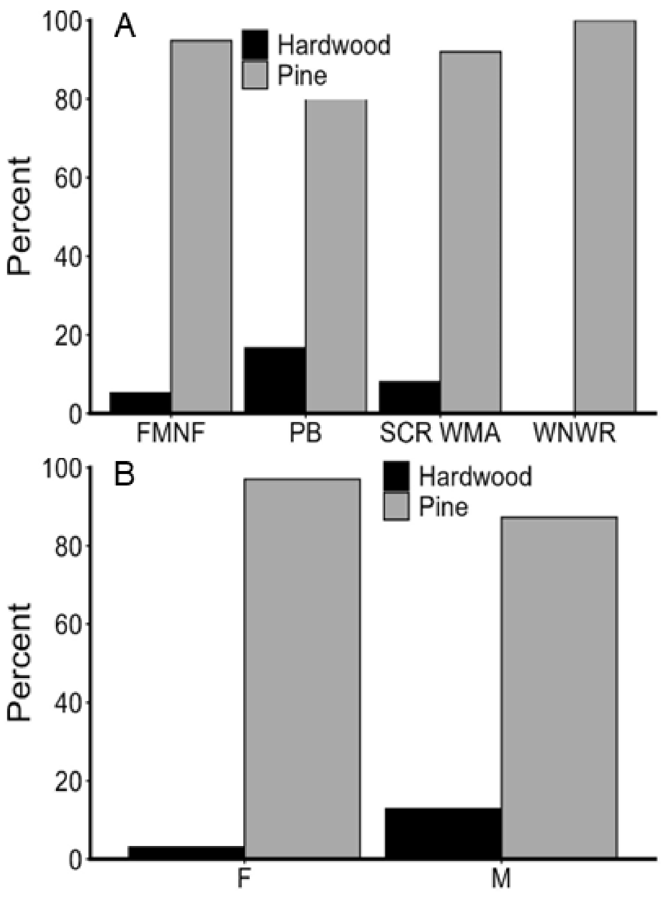

Figure 4. Tree species groups of day roosts used by Northern Long-eared Bats by A) study site, and B) sex (adults only) at Francis Marion National Forest (FMNF), Palmetto Bluff (PB), Santee Coastal Reserve Wildlife Management Area (SCR WMA), and Waccamaw National Wildlife Refuge (WNWR), in South Carolina, April–August 2017–2024.

live-damaged and 18.2% were dead. Most snags were pines (3 Longleaf and 14 Loblolly), although 1 was a Southern Red Oak. The proportion of roosts that were alive, live-damaged, or dead varied by site ($\chi^2 = 13.58$, df = 6, P = 0.03). This difference was driven, to some extent, by the WNWR site, where there were only 4 roosts, 2 of which were snags. In contrast, all roosts at PB and most at SCR WMA were alive (Fig. 5A). The proportion of roosts that were snags also varied between adult males and females ($\chi^2 = 11.19$, df = 2, P = 0.004), with adult females more likely to use snags (Fig. 5B).

Roost tree DBH was 30.3 ± 12.5 cm (median = 29.0 cm, range = 9.7–81.2 cm) and height was 19.4 ± 6.2 m (median = 18.6 m, range = 3.7–34.7 m). Median DBH differed among sites ($\chi^2 = 22.30$, df = 3, P < 0.0001). Roost trees had larger DBH at SCR WMA than at FMNF

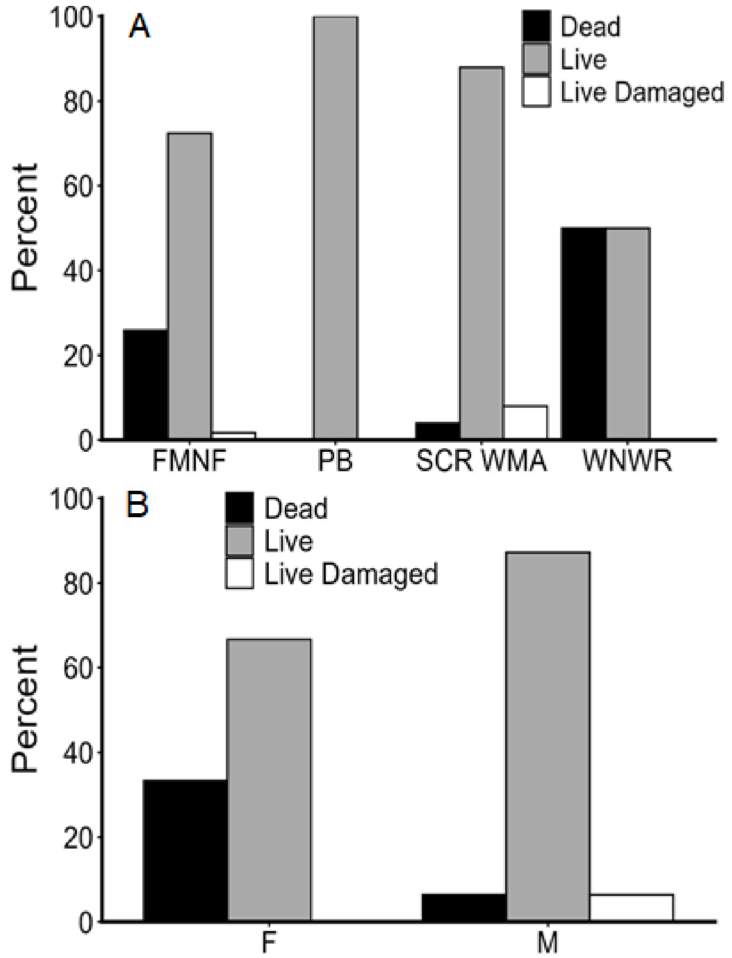

Figure 5. Decomposition state of day roosts used by Northern Long-eared Bats by A) study site, and B) sex (adults only) at Francis Marion National Forest (FMNF), Palmetto Bluff (PB), Santee Coastal Reserve Wildlife Management Area (SCR WMA), and Waccamaw National Wildlife Refuge (WNWR), in South Carolina, April–August 2017–2024.

(Table 1). Median tree height also differed among sites ($\chi^2 = 10.92$, df = 3, P < 0.01), with PB having taller trees than at FMNF and SCR WMA. Tree DBH and height did not differ between adult male and female roosts (P > 0.10; Table 2).

We determined roost type in 70 cases. In 36 cases, bats roosted under sloughing bark, whether the tree was dead or alive. Roosting sites also were in cracks or behind bark of dead branches (n = 28), and cavities (n = 6). Roost type varied among study sites ($\chi^2 = 26.10$, df = 4, P < 0.0001). Bats at PB and SCR WMA roosted under sloughing bark or in cavities on the bole, whereas bats at FMNF primarily used sloughing bark on the bole, or sloughing bark or cracks in dead branches; a few used cavities in the bole (Fig. 6A). Roosting sites in live trees were primarily under bark of the bole (n = 28) or under the bark or in cracks in dead branches (n = 21), but cavities (n = 3) were also used. Roost locations in live damaged trees were in cavities (n = 2) and a dead branch, whereas roost sites in snags were under bark on the bole (n = 8), and under the bark or in cracks in a branch (n = 6), and a cavity. Types of roosting site used by adult males and females did not differ ($\chi^2 = 4.33$, df = 2, P = 0.11; Fig. 6B).

Roosts were primarily found in pine and pine-hardwood forests (Fig. 7A), and roost forest types varied across sites ($\chi^2 = 45.06$, df = 9, P < 0.0001). This difference was due primarily to greater use of pine-hardwood forests at SCR WMA compared to other sites. Use of forest types did not vary between adult females and males ($\chi^2 = 5.47$, df = 3, P = 0.14; Fig.

Table 1. Characteristics of roost trees used by Northern Long-eared Bats at 4 study sites in South Carolina, April–August 2017–2024. Medians with different superscript letters are statically different (P ≤ 0.5). FMNF = Francis Marion National Forest; PB = Palmetto Bluff; SCR WMA = Santee Coastal Reserve and Wildlife Management Area and WNWR = Waccamaw National Wildlife Refuge.

Characteristic	Area	*n*	Mean ± *SD*	Median	Minimum	Maximum
DBH (cm)	FMNF	58	25.9 ± 9.4	25.5[a]	9.7	48.8
	PB	12	40.8 ± 19.0	36.7[ab]	23.1	81.2
	SCR WMA	22	36.9 ± 9.7	37.0[b]	10.9	60.7
	WNWR	4	26.0 ± 12.2	24.5[ab]	13.4	41.7
Tree height (m)	FMNF	58	19.2 ± 7.0	18.0[ac]	3.7	34.7
	PB	12	22.6 ± 4.6	20.9[b]	16.1	30.7
	SCR WMA	13	18.3 ± 2.3	18.0[c]	16.0	22.0
	WNWR	4	15.9 ± 4.6	14.4[abc]	12.2	22.6
Canopy cover (%)	FMNF	55	59.7 ± 14.0	55[ab]	6	86
	PB	12	64.8 ± 9.2	68.5[a]	46	77
	SCR WMA	20	53.6 ± 11.3	53.5[b]	34	81
	WNWR	4	50.5 ± 5.2	50.5[ab]	46	55

7B). Canopy cover in roost stands was 58.6 ± 13.0% (median = 55, range = 6–86) and varied across sites (χ^2 = 13.51, df = 3, P = 0.004), with canopy cover being greater at PB than at SCR WMA (Table 1). Canopy cover of male and female roost sites did not differ (z = 0.61, P = 0.54; Table 2).

Most roosts (54.0%) were in stands burned within the past 4 years, and this did not vary among the 3 sites with prescribed fire data (χ^2 = 0.758, df = 2, P = 0.68; Fig. 8A). The use of burned stands for roosting did not vary between males and females (χ^2 = 0.002, df = 1, P = 0.966; Fig. 8B). For roosts in previously burned stands, 36.2% were burned within the same year; 36.2%, approximately 1 year prior to the study; 19.1%, 2 years prior; and the remaining 8.6%, 3 or 4 years prior. Three of the 4 confirmed maternity roosts at SCR WMA were in stands that had been burned that year, and the other was in a stand that had been burned the prior year. Neither of the 2 maternity roosts in FMNF were in recently burned stands.

Discussion

Our study greatly increases knowledge of Northern Long-eared Bat ecology in the southern Atlantic Coastal Plain. Prior to this study, Northern Long-eared Bats were only known from 1 location in South Carolina (White et al. 2018), and no information was available about their summer phenology and roosting ecology. Although Northern Long-eared Bats do not appear common, they are widespread and inhabit areas throughout the South Carolina coast. Further, we found evidence of reproducing populations. Our results suggest that pine forests, particularly Longleaf and Loblolly Pine forests, are important roosting sites, and that prescribed fire, a common coastal forest management practice, appears compatible with Northern Long-eared Bat persistence.

Parturition and lactation in Northern Long-eared Bats occurs between mid-May and mid-June, but can occur later in summer at northern latitudes (Caceres and Barclay 2000, Krochmal and Sparks 2007). Reproductive phenology can even vary within small geographic areas, such as a state, and may be related to temperature (Geluso et al. 2019). We captured pregnant females as early as late April, which is similar to the reproductive phenology of females in coastal North Carolina, and suggests that reproduction by Northern Long-eared Bats in this region may occur earlier than elsewhere on the continent.

Table 2. Characteristics of roost trees used by adult female and male Northern Long-eared Bats in South Carolina, April–August 2017–2024.

Characteristic	Sex	n	Mean ± SD	Median	Minimum	Maximum
DBH (cm)	Female	32	27.6 ± 12.6	28.0	9.7	60.7
	Male	47	30.7 ± 13.6	27.9	10.9	81.2
Tree height (m)	Female	29	17.9 ± 7.6	16.0	3.7	34.7
	Male	41	20.4 ± 5.3	19.4	7.9	33.5
Canopy cover (%)	Female	31	62.5 ± 14.3	65	34	85
	Male	45	58.9 ± 10.7	55	35	86

Prior to WNS, colony sizes in the heart of the Northern Long-eared Bat range were often large, containing as many as 60–88 bats (Foster and Kurta 1999, Menzel et al. 2002, Rojas et al. 2017). In contrast, colony sizes observed in our study were much lower (maximum = 12 bats), and similar to colony sizes in other parts of the range post-WNS (Burrell and Bergeson 2022, Gorman et al. 2022, Grider et al. 2021, Kalen et al. 2022). Summer maternity colony sizes based on 64 emergence observations in coastal North Carolina were also low (mean = 4.7 bats, range 2–8 bats), suggesting coastal populations of Northern Long-eared Bats are considerably smaller than in the heart of its range pre-WNS. Small colony sizes may be due to lower population densities and/or could be related to the higher

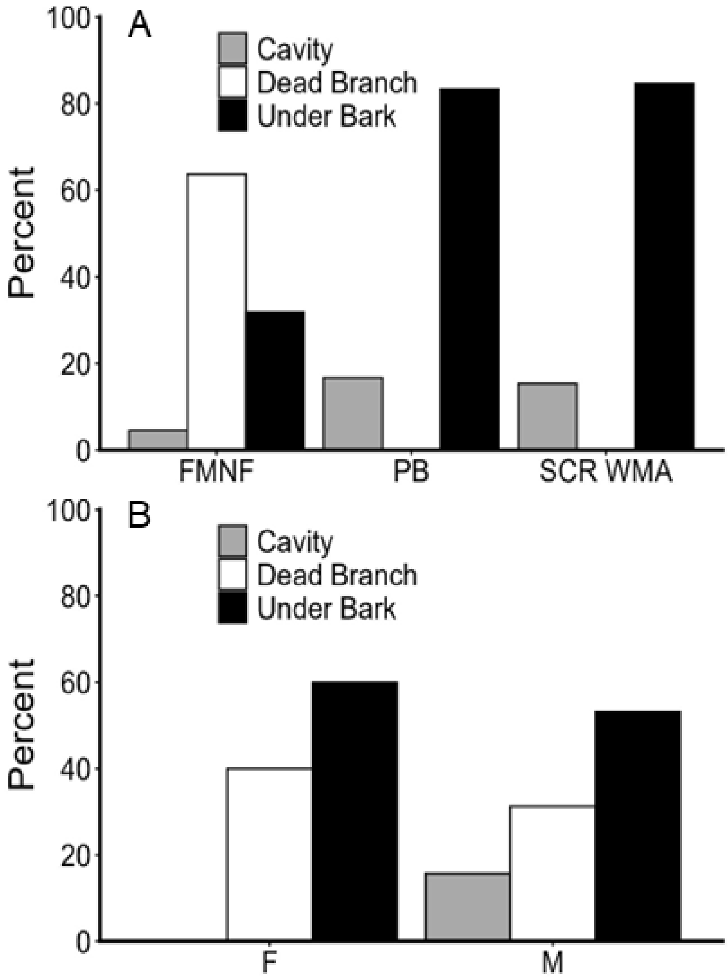

Figure 6. Types of day roosts used by Northern Long-eared Bats by A) study site, and B) sex (adults only) at Francis Marion National Forest (FMNF), Palmetto Bluff (PB), Santee Coastal Reserve Wildlife Management Area (SCR WMA), and Waccamaw National Wildlife Refuge (WNWR), in South Carolina, April–August 2017–2024.

temperatures in southern coastal regions that result in less need for social thermoregulation (Willis and Brigham 2007).

Northern Long-eared Bats in our study switched roosts approximately every 1–2 days and used an average of 3 roosts over the days they were tracked, which was in line with other studies throughout the species' range (Garcia et al. 2023). Similar to other findings (e.g., Foster and Kurta 1999, Gorman et al. 2023, Grider et al. 2021, Johnson et al. 2009), almost all Northern Long-eared Bat roosts were within 500 m of each other, and most were within 300 m of each other. The distance between capture sites and roosts was over 3 times greater than the distance among roosts, which indicated that Northern Long-eared Bats foraged well outside their roosting areas. For example, bats at SCR WMA often traveled >1 km between

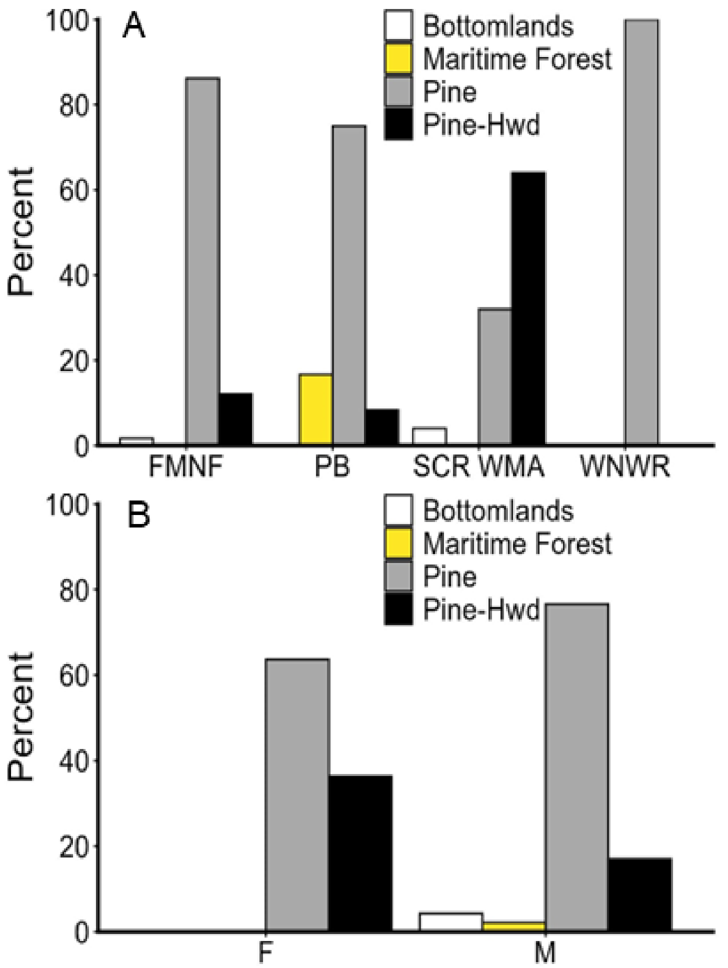

Figure 7. Roost forest types used by Northern Long-eared Bats by A) study site, and B) sex (adults only) at Francis Marion National Forest (FMNF), Palmetto Bluff (PB), Santee Coastal Reserve Wildlife Management Area (SCR WMA), and Waccamaw National Wildlife Refuge (WNWR), in South Carolina, April–August 2017–2024.

capture and roost sites, and were more likely to be captured in bottomland hardwood forests and riparian areas than bats at other sites. This suggests they may have used bottomland hardwood forests and riparian areas for foraging to a greater extent than bats at other sites and may have had to fly farther between bottomland hardwood forests or riparian areas and their roosts in pine forests. In contrast, bats at other sites roosted and foraged in pine and pine-hardwood forests. Despite the increased energetic costs associated with pregnancy (Kurta et al. 1989), 1 of the individuals that moved farthest was a pregnant female. Understanding the relationship between foraging and roosting habitats and the distribution of these habitats across the landscape, particularly for reproductive females, is necessary for developing better guidelines for Northern Long-eared Bat recovery.

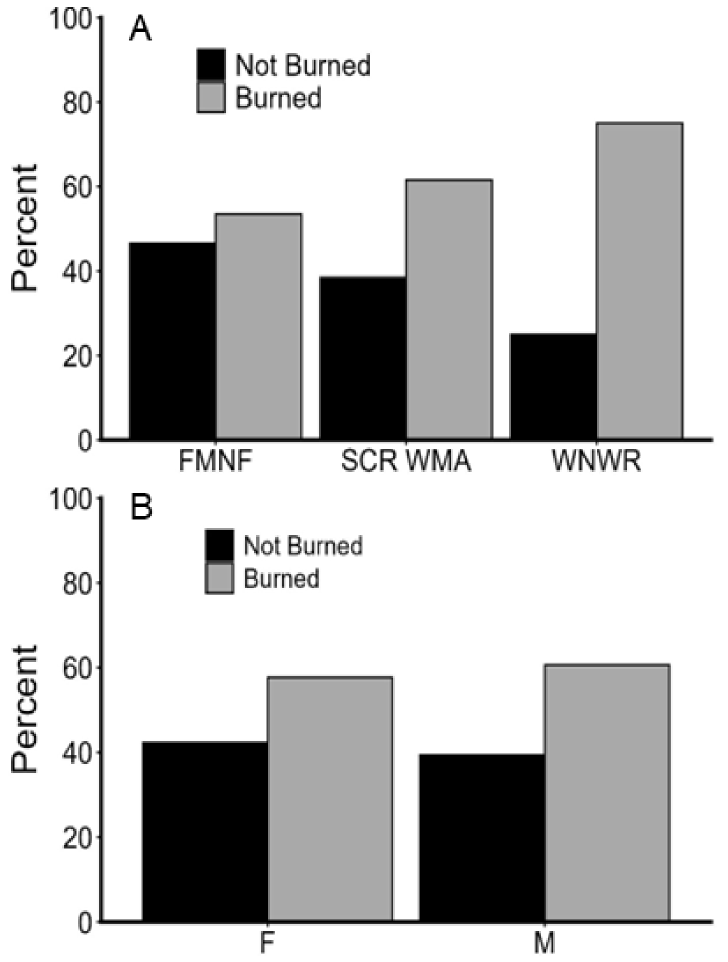

Figure 8. Use of burned and non-burned forest stands for roosting by Northern Long-eared Bats by A) study site, and B) sex (adults only) at Francis Marion National Forest (FMNF), Palmetto Bluff (PB), Santee Coastal Reserve Wildlife Management Area (SCR WMA), and Waccamaw National Wildlife Refuge (WNWR), in South Carolina, April–August 2017–2024.

Northern Long-eared Bats roosted primarily in tall live pines, and this was consistent across sites and between sexes. Early studies of Northern Long-eared Bats suggested they primarily roosted in hardwood trees (Caceres and Barclay 2000), but subsequent studies have shown that in some areas they mostly use conifers, particularly pines (Alston et al. 2019, Garcia et al. 2023, Perry and Thill 2007, Rojas et al. 2017). In contrast, maternity roosts of Northern Long-eared Bats in coastal North Carolina were mainly in hardwoods in wetland forests, although some Loblolly and Longleaf pines were also used (Jordan 2020). While both live and dead trees are used by Northern Long-eared Bats (Lacki et al. 2009a), most studies reported that they principally occupy snags (e.g., Alston et al. 2019, Burrell and Bergeson 2022, Grider et al. 2021, Perry and Thill 2007). In contrast, we found that in coastal South Carolina Northern Long-eared Bats primarily roosted in live trees, often using dead branches or sloughing bark, although adult females were more likely to be in snags. The use of predominantly live trees in our study may have been due to availability; however, without data on the availability of snags within South Carolina coastal forests, it is not possible to determine why live trees were occupied to a greater extent compared to other studies. Roost tree diameters in the current study were within the range reported for Northern Long-eared Bats (Garcia et al. 2023). In contrast, roost tree heights in our study tended to be at the upper end of the range, perhaps because bats in our study primarily occupied live trees. Nonetheless, bats roosted in a wide range of tree sizes (Table 1). Variation in roost tree characteristics across the Northern Long-eared Bat range may be related to differences in availability, microclimatic characteristics of trees, or structural characteristics of available roosting structures (Garcia et al. 2023, Silvis et al. 2016).

Given the high use of pines as roosts, it was not surprising that Northern Long-eared Bats in coastal South Carolina primarily used pine and pine-hardwood stands for roosting. Although there was a wide range of canopy cover in used stands (6–86%), the distribution was unimodal, with most roost stands having 50–60% canopy cover. This contrasts with the distribution of canopy cover at Northern Long-eared Bat roosts in Michigan, which was bimodal (i.e., either 0–20% or 80-100%; Foster and Kurta 1999). Other studies found mean canopy covers that were either lower (≤ 46%) than we observed (Alston et al. 2019, Burrell and Bergeson 2022, Carter and Feldhamer 2005, Garcia et al. 2023, Rojas et al. 2017), or higher (≥ 66%) than we observed (Broders and Forbes 2004, Lacki and Schwierjohann 2001, Menzel et al. 2002, Perry and Thill 2007). Canopy cover may impact microclimate by affecting the amount of solar radiation on a roost (Bergeson et al. 2021). Reproductive females often select roosts with lower canopy cover to maximize solar radiation, which allows them to reduce the energetic demands of thermoregulation while devoting energy to gestation and lactation. In contrast, males and non-reproductive females during spring and fall often select roosts with higher canopy cover, which facilitates the use of torpor (Dzal and Brigham 2013, Hamilton and Barclay 1994). However, we found no difference in canopy cover of roost stands used by adult males and females. Future research may consider how canopy cover at or immediately surrounding roosts affects roost use and selection instead of at the larger scale (30-m cell) that we used. This may be especially relevant given the high temperatures that Northern Long-eared Bats experience at the southern portion of their range.

Pine forests of the southeastern Coastal Plain have a long history of frequent fires and are currently maintained through frequent use (1–4 years) of low-intensity fire (Glitzenstein et al. 2021). Thus, Northern Long-eared Bats in the Coastal Plain may be well-adapted to fire and the forest structure it creates. Over half the roosts we found at the 3 sites with fire history data (FMNF, SCR WMA, and WNWR) were in stands burned within the past 5 years, demonstrating Northern Long-eared Bats readily used recently burned sites. In other studies, Northern Long-eared Bats often responded to prescribed fire in a neutral or positive way in regard to roost use and selection (Ford et al. 2016) and often roosted in previously burned areas (Johnson et al. 2009, Lacki et al. 2009b), even some that were burned a few days earlier (Dickinson et al. 2009). Many bats in our study, including reproductive females, roosted in stands that had burned earlier in the year.

Prescribed fire may be beneficial for roosting bats because it creates canopy gaps that increase solar radiation, reducing energy demands for reproductive females and their young (Boyles and Aubrey 2006). Fire may also reduce clutter in the midstory and create cracks or crevices in the boles or branches of live trees, which can be used for roosting (Perry 2012). Fire may also increase the number of Loblolly Pine snags (Zarnoch et al. 2014), although it had no effect on pine snag density in Alabama (Baldwin et al. 2023).

Adult males and females generally had similar roosting patterns, but we found some differences. For example, females were more likely to use snags than males. Four of the 9 roosts that we inferred were maternity colonies were in snags. Other maternity roosts were in dead branches of live trees. Snags with sloughing bark are the most common roost type used by maternity colonies of Northern Long-eared Bats across their range (Lacki et al. 2009a), and they may be particularly important for female bats in the South Carolina Coastal Plain. We also found that the distance among roosts was greater for males than females, similar to Northern Long-eared Bats in coastal New England (Hoff et al. 2024). This contrasts with New Brunswick, where the distance between successive roosts and minimum roosting areas were greater for females than males (Broders et al. 2006). Snags are often aggregated on the landscape (Kroll et al. 2012); hence, female bats may be selecting areas with high snag densities, resulting in shorter movements. Further, lactating females must carry non-volant young when they switch roosts, so choosing areas with closer roosts may help reduce energetic costs of roost switching.

Populations of Northern Long-eared Bats have declined throughout much of their range as a result of WNS (Cheng et al. 2021), except in coastal regions where WNS does not occur (Hoff et al. 2024). Our data suggest that pine and pine-hardwood forests are particularly important for spring and summer roosting in coastal South Carolina. Although bats used live trees to a greater extent than dead trees, snags may be particularly important for maternity colonies. As with most other tree-roosting species (Barclay and Kurta 2007, Carter and Menzel 2007), many trees will be needed to support bats throughout the active season due to their propensity to switch roosts every 1–2 days. Finally, the relationship between Northern Long-eared Bat summer roost use and prescribed fire needs to be explored. Many types of wildlife are associated with, or depend on, fire-maintained pine forests in the Coastal Plains (Glitzenstein et al. 2021), some of which are threatened or endangered, such as *Dryobates borealis* (Vieillot) (Red-cockaded Woodpecker) and *Ambystoma cingulatum* Cope (Frosted Flatwoods Salamander), or are species of concern such as *Gopherus polyphemus* (Daudin) (Gopher Tortoise) and *Sciurus niger niger* L. (Southeastern Fox Squirrel). Because coastal populations of Northern Long-eared Bats may be critical to the species' survival, managing them in the Coastal Plain will require balancing the requirements of all species on a spatial and temporal basis.

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