Seasonal Activity Patterns of Northern Long-eared Bats on the Coastal Mid-Atlantic

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Abstract: Conservation of bats declining from white-nose syndrome (WNS) impacts requires an understanding of both temporal and landscape-level habitat relationships. Traditionally, much of the research on bat ecology has focused on behavior of summer maternity colonies within species' distribution cores, including that of the endangered northern long-eared bat (*Myotis septentrionalis*). To further our knowledge of this species, we evaluated multi-season activity patterns in eastern North Carolina and Virginia, including areas where populations were recently discovered. We used passive acoustic monitoring to assess relative and probable activity of northern long-eared bats from October 2016 to August 2021. Northern long-eared bat relative activity was greatest in areas containing greater proportions of woody wetlands and upland pine-dominated evergreen forests. However, the likelihood of recording northern long-eared bats was associated with smaller proportions of woody wetlands and open water resources. Furthermore, we observed a higher probability of recording northern long-eared bats during non-winter seasons. Probable activity was greatest at temperatures between 10 and 25 C, potentially highlighting an optimal thermoneutral zone for the species regionally. Relative activity of northern long-eared bats on the Coastal Plain of Virginia and North Carolina was primarily driven by cover features, whereas probable activity was driven by a combination of cover features, seasonality, and temperature. Therefore, acoustical surveys for this species may be most effective when targeting woody wetlands adjacent to upland forests, particularly upland pine-dominated evergreen stands, during moderate temperatures of non-winter seasons (1 April–15 November). Moreover, conservation of a diverse mosaic of woody wetlands juxtaposed by upland forests may promote both roosting and overwintering habitat, thereby enhancing overwintering survival, maternity colony establishment, and ultimately, successful reproduction of northern long-eared bats.

Key words: *Myotis septentrionalis*, coastal, seasonal, activity

Several North American bat species have experienced severe population declines as a result of the introduction of *Pseudogymnoascus destructans* (*Pd*), the fungal pathogen that causes white-nose syndrome (WNS; Cheng et al. 2021). In the Central and Southern Appalachians of the U.S., the northern long-eared bat (*Myotis septentrionalis*) was one of the most commonly occurring species pre-WNS (Ford et al. 2006, Rojas et al. 2017). In regions that experience harsh winters and lengthy hibernation periods, such as the High Allegheny Plateau of the Central Appalachians, northern long-eared bat populations precipitously decreased once *Pd* invaded karst hibernacula (Johnson et al. 2013, Ford et al. 2016, Austin et al. 2018). Additionally, the recently documented abandonment of maternity colony roosts and lack of juvenile captures in Virginia's Ridge and Valley and Blue Ridge Mountains (Figure 1) provide further evidence suggestive of population collapse (Kalen et al. 2022). These declines threaten the species with extinction (Cheng et al. 2021), contributing to a 2015 threatened listing under the U.S. Endangered Species Act of 1973 (USFWS 2015) and recent uplisting to endangered (USFWS 2022).

Despite widespread declines in the interior Northeast and Mid-Atlantic of the U.S. (Figure 1), isolated, remnant populations of northern long-eared bats appear to persist in coastal environments along the Eastern Seaboard (Jordan 2020, Deeley et al. 2021, De La Cruz et al. 2022b, Montgomery and Hogue 2022, Garcia
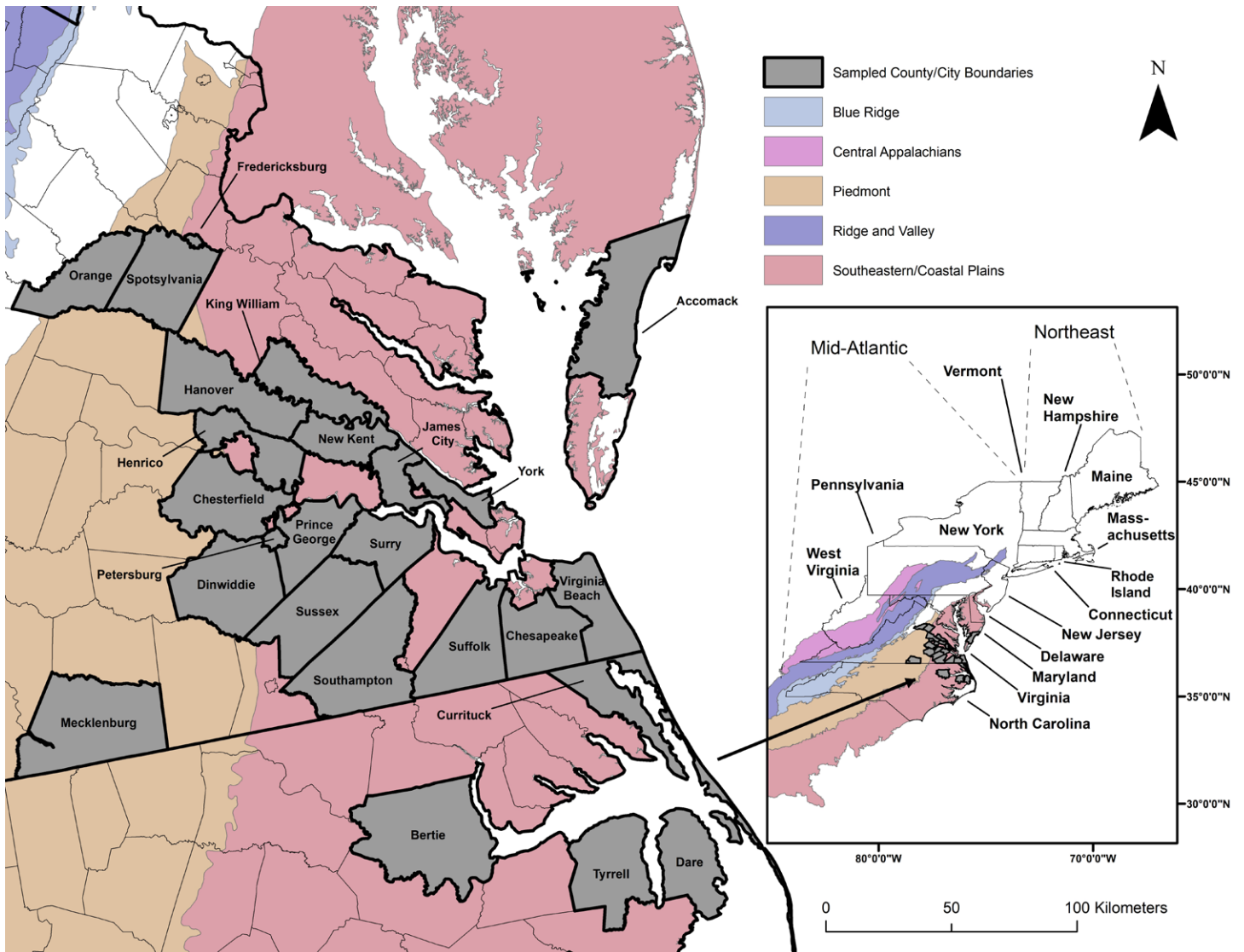
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Figure 1. County and city boundaries in northeastern North Carolina and southeastern Virginia, containing 179 acoustic sites surveyed for northern long-eared bat (*Myotis septentrionalis*) calls, 2016–2021.

et al. 2023, Gorman et al. 2023, Hoff et al. 2023). Some of these populations have relied on the use of unique, sparsely occupied, and/or non-contaminated hibernacula as overwintering habitat. For example, in coastal Massachusetts, northern long-eared bats hibernate in the basements and crawlspaces of homes and military bunkers on Nantucket Island (Hoff et al. 2023). However, in coastal Virginia, male northern long-eared bats use woody wetlands and the intersection of these riparian forests and upland pine forests as overwintering habitat (De La Cruz et al. 2022b). Jordan (2020) documented the year-round presence of northern long-eared bats on the Coastal Plain of North Carolina. These bats largely used swamp tupelo (*Nyssa biflora*), water tupelo (*N. aquatica*), bald cypress (*Taxodium distichum*), and red maple (*Acer rubrum*) in

contiguous tracts of woody wetlands as torpor sites during winter. Within the upper Gulf Coastal Plain of Louisiana, northern long-eared bats select tall, large-diameter pines with exfoliating bark as winter roosts (Garcia et al. 2023). In contrast, overwintering habitat in and adjacent to the Washington, D.C. metropolitan region (Deeley et al. 2021) may consist of a combination of alternative hibernacula such as mines (Lituma et al. 2021) and coastal forest torpor sites (Jordan 2020), or bats exhibit latitudinal migration, as observed in tricolored bats (*Perimyotis subflavus*; Fraser et al. 2012).

Historically, in the Mid-Atlantic, northern long-eared bats were assumed to range no farther south and east than the Great Dismal Swamp in southeastern Virginia (Morris et al. 2009). Furthermore,

the species was also assumed to hibernate exclusively in cracks and crevices of caves or mines during winter (Caceres and Barclay 2000), features rare in the Coastal Plain. However, recent research has revealed both summer maternity colonies and overwintering populations of northern long-eared bats in southeastern Virginia (De La Cruz et al. 2022b) and eastern North Carolina (Jordan 2020). Specifically, populations were first discovered in the Coastal Plain of North Carolina in 2007 (Morris et al. 2009) and, as of 2020, 181 unique northern long-eared bats have been captured in this area (Jordan 2020). In Virginia and North Carolina, only in coastal areas have colonies remained cohesive and reproductively successful (Jordan 2020, De La Cruz et al. 2022a). Assuming continued declines of northern long-eared bat populations associated with inland hibernacula, these isolated, coastal populations may provide the last remaining refugia for the species in the Mid-Atlantic.

The persistence of northern long-eared bat populations in the coastal Mid-Atlantic underscores the need for a comprehensive understanding of their seasonal activity patterns in response to weather conditions to inform effective conservation efforts. In coastal North Carolina, northern long-eared bats were observed active throughout the winter but entered short bouts of torpor during periods of near-freezing weather (Jordan 2020). In coastal Massachusetts, the hibernation period of northern long-eared bats is shorter than mainland counterparts, likely due to more nights above freezing at coastal sites (Hoff et al. 2023). During summer in coastal New York, Gorman et al. (2021) found that northern long-eared bats were more active during warmer nights but that individuals were not deterred by precipitation events or excessive wind. Although a growing body of literature has examined northern long-eared bat ecology in coastal habitats of the Northeast and Mid-Atlantic (Jordan 2020, Gorman et al. 2021, Gorman et al. 2022, Gorman et al. 2023, De La Cruz et al. 2022a, Hoff et al. 2023), no research has evaluated the seasonal activity of northern long-eared bats using passive acoustic methods in northeastern North Carolina and southeastern Virginia. To examine this seasonal activity, we undertook a multi-season survey to assess relative (i.e., weekly counts of echolocational recordings) and probable (i.e., likelihood to collect ≥1 recording) activity of northern long-eared bats in relation to biotic and abiotic factors across southeastern Virginia and northeastern North Carolina. Our objectives were to use passive acoustic monitoring to 1) identify bat presence across the study area; 2) assess the effect of cover type covariates; 3) examine effects of weather and seasonality; 4) and identify potential conservation needs to enhance management efforts for northern long-eared bats within the region. We hypothesized that northern long-eared bat activity would be spatially concentrated and highest during the non-winter season (1 April–15 November), during

warmer and drier weather, and in contiguous tracts of woody wetlands and upland forests. Additionally, we hypothesized that the likelihood to record northern long-eared bat activity would follow similar trends.

Study Area

Our study area encompassed 23 counties and 2 independent cities in the lower Piedmont and Coastal Plain of northeastern North Carolina and southeastern Virginia (Figure 1). The Piedmont is comprised of narrow to broad upland ridgetops ranging in elevation from 100 m to 400 m. The region experiences an average annual temperature of 12–18 C and receives 100–180 cm of precipitation per year. Pine stands (*Pinus* spp.), including loblolly pine (*P. taeda*) and shortleaf pine (*P. echinata*), are dominant on eroded sites, whereas hardwoods and mixed stands, often comprised of white oak (*Quercus alba*), red oak (*Q. rubra*), and sweetgum (*Liquidambar styraciflua*), occur on less eroded sites and bottomlands (USDA NRCS 2022). The Coastal Plain ranges in elevation from approximately 180 m at the Fall Line (i.e., boundary with Piedmont), where the landscape is characterized by short, steep slopes adjacent to bottomlands, to sea level at the Atlantic Ocean, where broad peneplains bisected by stream channels predominate. The Coastal Plain receives approximately 100–160 cm of precipitation and experiences an average annual temperature of 13–21 C (USDA NRCS 2022). Upland forests of the Coastal Plain are dominated by a mixed oak-hickory (*Carya* spp.)-pine community, which historically included a large component of longleaf pine (*P. palustris*). Periodically flooded forests adjacent to sediment-laden brownwater rivers that originate in the Appalachians or Piedmont are often comprised of swamp chestnut oak (*Q. michauxii*), cherrybark oak (*Q. pagoda*), shagbark hickory (*C. ovata*), and sweetgum (Fleming and Patterson 2017). Alluvial woody wetlands associated with acidic blackwater rivers that originate on the Coastal Plain are primarily composed of water tupelo, swamp tupelo, and bald cypress (Fleming and Patterson 2017). Large acreage of native forest and wetland habitats on the Coastal Plain of North Carolina and Virginia have been converted to agricultural fields and short-rotation pine plantations (Hefner et al. 1994, Hunter et al. 2001).

Methods
Acoustic Monitoring

We conducted acoustic monitoring at 179 sites from October 2016 to August 2021 (Figure 2). We deployed zero-crossing ultrasonic recorders (Song Meter 2 and Song Meter 4; Wildlife Acoustics, Maynard, Massachusetts), fitted with microphones (SMM-U1) to collect acoustic data. We attached recorders to trees at an approximate height of 1.5 m above the ground, ensuring
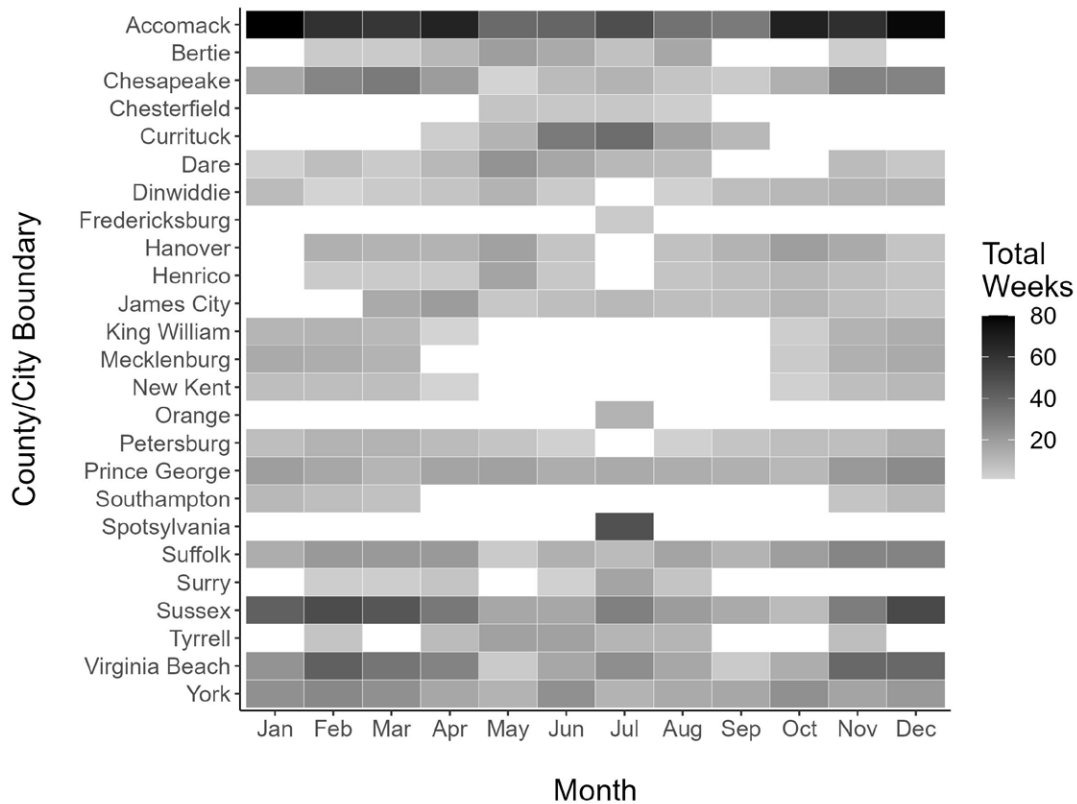
Figure 2. Sampling effort as represented by a monthly heatmap (white areas represent unsampled months) of the total number of acoustic monitoring weeks conducted in eastern North Carolina and Virginia, 2016–2021 (see Figure 1 for county/city locations).

microphones extended beyond the diameter of the bole, or on 3-m poles as dictated by site conditions (De La Cruz and Ward 2016). We deployed acoustic recorders near forest canopy openings, water sources, tree lines adjacent to large openings or that connected two larger blocks of forest, potential roost trees, and road and/or stream corridors with open tree canopies to assess both the relative and probable activity of northern long-eared bats (Britzke et al. 2010). To mitigate spatial autocorrelation, we deployed recorders at widely spaced sites, observing a median distance of 610 m between sampling sites. We programmed detectors to record from sunset to sunrise. We checked functionality of recorders and downloaded and processed data at approximately 30- to 60-day intervals. We identified echolocational recordings to species with automated acoustic software (Kaleidoscope Pro software; v. 5.4.7; Wildlife Acoustics), using default signal detection parameters and the 5.4.0 classifier set at 'Balanced/Neutral' (USFWS 2020). Based on geographical range extents (Reid 2006), we considered the following species for presence: Rafinesque's big-eared bats (*Corynorhinus rafinesquii*), big brown bats (*Eptesicus fuscus*), eastern red bats (*Lasiurus borealis*), hoary bats (*Lasiurus cinereus*), silver-haired bats (*Lasionycteris noctivagans*), Southeastern myotis

bats (*M. austroriparius*), little brown bats (*M. lucifugus*), evening bats (*Nycticeius humeralis*), and tricolored bats (*Perimyotis subflavus*). We also included Brazilian free-tailed bats (*Tadarida basiliensis*), Indiana bats (*M. sodalis*), northern long-eared bats, and Seminole bats (*Lasiurus seminolus*) due to recently documented range expansions into the Coastal Plain of Mid-Atlantic states (St. Germain et al. 2017, McCracken et al. 2018, Jordan 2020, True et al. 2021).

Predictor Variables

In response to recent research in the southeastern Coastal Plain (Jordan 2020, Stevens et al. 2020, De La Cruz et al. 2022a, Garcia et al. 2023), we assessed relative and probable activity of northern long-eared bats in relation to percent cover of woody wetlands (i.e., ≥20% forest/shrubland periodically saturated with water), evergreen forests (i.e., ≥20% forested area containing trees ≥5 m in height; ≥75% of foliage maintained all year), and open water (i.e., open water areas containing <25% vegetation or soil) resources using the 2019 National Land Cover Database (NLCD) raster dataset (Dewitz and USGS 2021). Additionally, we examined the effect of forest fragmentation on relative activity and the

probability to record northern long-eared bat calls (De La Cruz et al. 2022a). To incorporate the availability of large core forests (>200 ha) in our models, we used a mapping tool (Landscape Fragmentation Tool in ArcGIS; Vogt et al. 2007) to characterize a forest/non-forest raster dataset derived from NLCD data. We also assessed canopy height (EROSC 2019), a known factor influencing seasonal and spatial habitat selection by northern long-eared bats (Perry and Thill 2007, De La Cruz et al. 2022a). We standardized all raster datasets to a 100-m resolution and, based on foraging dispersal estimates of northern long-eared bats (Silvis et al. 2016), calculated focal means of these raster data using a 500-m moving window analysis (De La Cruz et al. 2023). We also assessed the impact of weather variables on the relative and probable activity of northern long-eared bats. These variables included the weekly mean of daily total precipitation (mm) and, assuming upper thermal limits (Patriquin et al. 2016), the quadratic relationship of the weekly mean of daily average temperature (C). We obtained matching nightly weather data for sites from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) Data Explorer, using the inverse-distance squared weighting interpolation option for the standard 4 km PRISM grid cell (PRISM Climate Group 2022). Recognizing the high correlation between date and included quadratic temperature trends, we analyzed the simple effects of non-winter and winter seasons (1 April–15 November; 16 November–31 March) on northern long-eared bat activity.

Statistical Analysis

We assumed presence of northern long-eared bats for automated identification only if a statistically significant maximum likelihood estimate (MLE; $P < 0.05$) was observed for any given site-night, thereby accounting for known rates of misclassification and minimizing false positive and false negative errors (Britzke et al. 2002). We then aggregated these nightly data by site and year and totaled counts for northern long-eared bats across each corresponding week of the year (Straw et al. 2022). We used these counts (i.e., weekly relative activity) as the response variable in all modeling efforts. We used a Shapiro-Wilk test to assess weekly relative activity for non-normality and discovered that data were not ($P < 0.01$) normally distributed (R Core Team 2020). Consequently, we used zero-inflated negative binomial generalized linear mixed models (GLMMs) in the glmmTMB R package (Brooks et al. 2017) for all statistical analyses. All GLMMs included two sub-models: 1) a conditional count sub-model to model relative activity; and 2) a zero-inflation sub-model to model probable activity. Prior to modeling, we checked for collinearity across predictor variables using pairwise correlation (threshold = $|0.8|$) and scaled and centered continuous variables. In total, we compared eight GLMMs, including a null model. In our seven multivariate models, we matched predictor variables in the conditional and zero-inflation sub-models. We included in all models the spatial random effect of recorder site and temporal random effect of year (Carlin and Chalfoun 2021, Taylor et al. 2023); however, we excluded the random effects of site and year from all zero-inflation sub-models. To rank models, we used Akaike Information Criterion corrected for small sample size (i.e., AIC_c). We defined the top-ranking model as that which had no competing model within two ΔAIC units (Burnham and Anderson 2002). We used the DHARMa package in R to assess our top model for goodness-of-fit and over- and under-dispersion using a quantile-quantile plot, residual plot, and a one-sample Kolmogorov-Smirnov test (Hartig 2020). Furthermore, we investigated the ecological significance of our top model using the performance package in R to calculate the conditional (i.e., the proportion of variance explained by fixed and random factors) Nakagawa R^2 (Nakagawa and Schielzeth 2013, Lüdecke et al. 2021). We interpreted R^2 values as follows: ≤0.20, very low; 0.21–0.40, low; 0.41–0.60, medium; 0.61–0.80, high; and 0.81–1.00, as very high proportions of variance explained (Gorman et al. 2021, Hill et al. 2024, Torre et al. 2022). Finally, we investigated the relationship between relative and probable activity and significant predictor variables using partial effect plots.

Results

During 2016–2021, we sampled for 3312 weeks and collected 6,056,851 acoustic data files from 179 acoustic sampling sites in northeastern North Carolina and southeastern Virginia. Based on nights displaying a significant ($P < 0.05$) MLE, we identified 616,775 (10%) files to species, including 5273 (<1%) files identified as northern long-eared bats. We recorded northern long-eared bats in 72% of sampled county and city boundaries, including all counties in North Carolina. Our highest northern long-eared bat call totals were collected in Sussex ($n = 1676$; $\bar{x} = 140$ per site), Chesapeake ($n = 880$; $\bar{x} = 176$ per site), and Virginia Beach ($n = 298$; $\bar{x} = 37$ per site) counties, Virginia, and Currituck County ($n = 1525$; $\bar{x} = 169$ per site), North Carolina. We recorded no northern long-eared bats in Chesterfield, Henrico, King William, Mecklenburg, and Orange counties, Virginia, or within the cities of Fredericksburg and Petersburg, Virginia.

We had no competing models within two $ΔAIC_c$ units and therefore consider our top-ranking model to be the best supported (Table 1). Our top model passed all DHARMa goodness-of-fit tests and explained a high proportion of variance ($R^2 = 0.69$), suggesting strong ecological relevance. We observed that northern long-eared bat weekly relative activity was greatest in areas containing larger proportions of woody wetlands and evergreen forests (Table 2;

Table 1. Variables included in both conditional count and zero-inflation sub-models of generalized linear mixed models, number of full-model parameters (K), Akaike's information criterion (AIC$_c$) units, ΔAIC$_c$ units, full-model weights (w_i), and full-model log-likelihood (LL), predicting weekly relative and probable activity of northern long-eared bats (*Myotis septentrionalis*) in northeastern North Carolina and southeastern Virginia, 2016–2021.

Model[a]	K[b]	AIC$_c$	ΔAIC$_c$	w_i	LL
TEMP + TEMP² + PRECIP + WOODY + EVER + WATER	19	3044.37	0.00	0.93	−1503.07
TEMP + TEMP² + PRECIP + WOODY + EVER + WATER + LARGE + CANOPY	23	3049.49	5.12	0.07	−1501.58
TEMP + TEMP² + PRECIP + LARGE + CANOPY	17	3058.83	14.46	0.00	−1512.32
TEMP + TEMP² + PRECIP	13	3061.97	17.6	0.00	−1517.93
WOODY + EVER + WATER	13	3079.15	34.78	0.00	−1526.52
WOODY + EVER + WATER + LARGE + CANOPY	17	3079.52	35.15	0.00	−1522.67
LARGE + CANOPY	11	3090.35	45.97	0.00	−1534.13
Null	3	3466.75	422.38	0.00	−1730.37

a. TEMP + TEMP²: quadratic polynomial of the weekly mean of daily average temperature (C); PRECIP: weekly mean of daily total precipitation (mm); WOODY: percent woody wetlands; EVER: percent evergreen forests; WATER: percent open water; LARGE: percent core forest (>200 ha); CANOPY: canopy height (m).

b. All models included a single dispersion parameter and intercepts in both the conditional and zero-inflation sub-models. Excluding the Null model, each conditional count sub-model contained the fixed effect of season and random effects of site and year, while zero-inflation sub-models included only the fixed effect of season.

Table 2. Predictor variables, *β* and SE estimate, *z*-values, *P*-values, and lower (LCL) and upper confidence limits (UCL) for the top generalized linear mixed model predicting weekly relative (i.e., counts of echolocational recordings; conditional sub-model) and probable (i.e., likelihood to collect ≥1 recording; zero-inflation sub-model) activity of northern long-eared bats (*Myotis septentrionalis*) in northeastern North Carolina and southeastern Virginia, 2016–2021.

Sub-model	Term[a]	*β*	SE	*z*	*P*	LCL	UCL
Conditional	Intercept	−3.93	0.82	−4.82	<0.01	−5.53	−2.34
	TEMP	24.20	18.03	1.34	0.18	−11.13	59.53
	TEMP²	−22.90	13.15	−1.74	0.08	−48.68	2.88
	PRECIP	−0.15	0.12	−1.22	0.22	−0.38	0.09
	WOODY	1.78	0.44	4.06	<0.01	0.92	2.63
	EVER	1.16	0.46	2.52	0.01	0.26	2.06
	WATER	−0.08	0.48	−0.18	0.86	−1.02	0.85
	SEASON − Winter	0.26	0.42	0.61	0.54	−0.57	1.08
Zero-inflation	Intercept	−0.69	0.30	−2.34	0.02	0.11	1.25
	TEMP	13.30	13.47	0.99	0.32	−38.26	13.78
	TEMP²	−34.39	9.56	−3.60	<0.01	16.12	53.63
	PRECIP	−0.05	0.12	−0.39	0.69	−0.18	0.28
	WOODY	−0.28	0.14	−2.01	0.04	0.00	0.55
	EVER	−0.01	0.11	−0.12	0.90	−0.20	0.22
	WATER	−0.60	0.20	−3.02	<0.01	0.21	0.98
	SEASON − Winter	−0.79	0.38	−2.09	0.04	0.11	1.25

a. TEMP and TEMP²: terms of the quadratic polynomial effects of weekly mean of daily average temperature (C); PRECIP: weekly mean of daily total precipitation (mm); WOODY: percent woody wetlands; EVER: percent evergreen forests; WATER: percent open water; SEASON – Winter: fixed effect of the winter season; the conditional sub-model contained the random effects of site location and year.

Figure 3. Partial effect plots of predicted weekly relative activity (and 95% CI) of northern long-eared bats (*Myotis septentrionalis*) in eastern North Carolina and Virginia, 2016–2021.

Figure 3). However, we observed no influence of temperature, precipitation, open water, or season on relative activity of the species (Table 2). Our results indicated that northern long-eared bat activity was more likely to be documented in non-winter seasons and during moderate temperature conditions (Table 2; Figure 4). We also observed that northern long-eared bats were more likely to be recorded in areas containing little open water and lesser amounts of woody wetland cover (Table 2; Figure 4). Finally, we observed
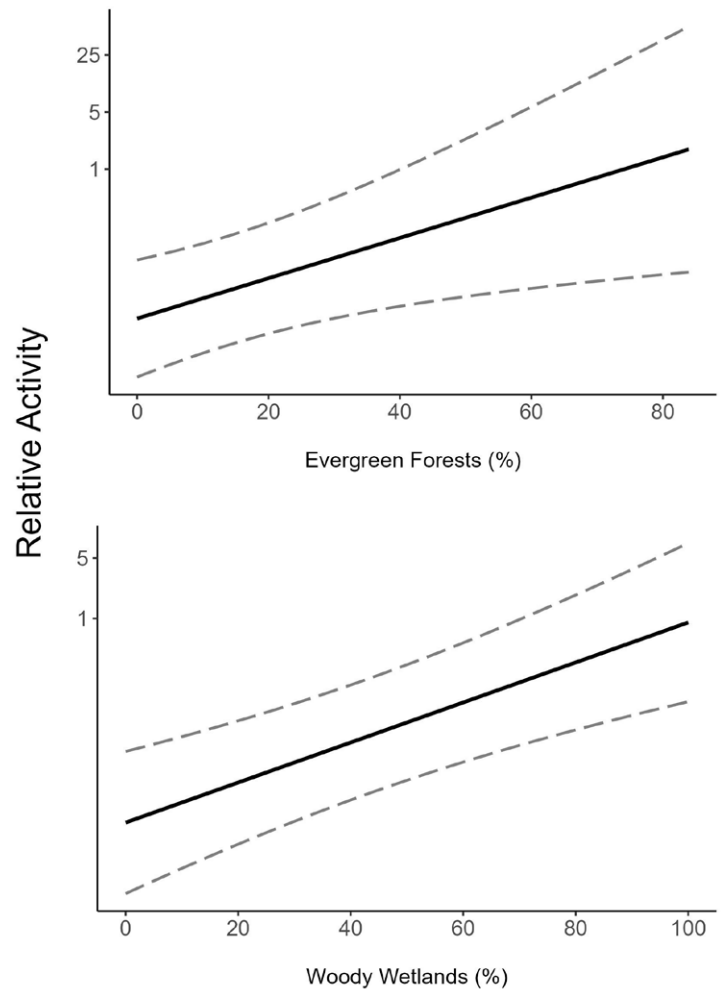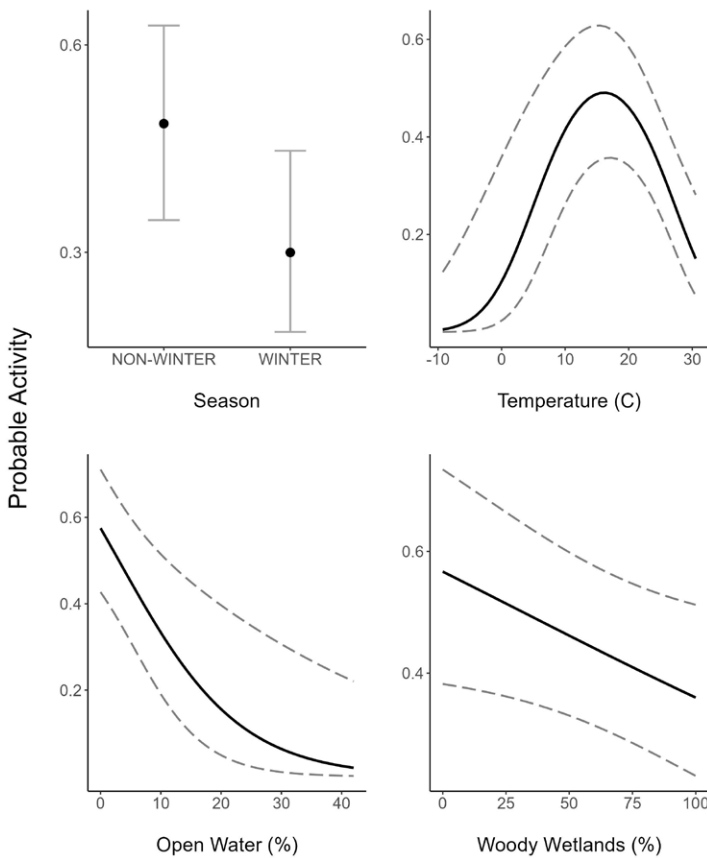
Figure 4. Partial effect plots of weekly predicted probability of activity (and 95% CI) of northern long-eared bats (*Myotis septentrionalis*) in eastern North Carolina and Virginia from 2016 to 2021 (non-winter = 1 April–15 November; winter = 16 November–31 March).

no relation between probable activity of northern long-eared bats and precipitation or evergreen forest cover (Table 2).

Discussion

Northern long-eared bats, widely regarded as a forest obligate, have been shown to select deciduous forests over pine forests across much of their range (Silvis et al. 2016). Our findings, however, indicate that northern long-eared bats in northeastern North Carolina and southeastern Virginia are more active in landscapes with higher proportions of woody wetlands and upland pine-dominated evergreen forests. However, probable activity decreased with increasing woody wetland cover and open water. Although northern long-eared bats do use woody wetlands for both roosting and foraging, our results suggest that northern long-eared bats may rely on those areas of woody wetlands more associated with upland forests rather than semi- or permanently inundated cover. For example, in the Coastal Plain of North Carolina, core and peripheral home ranges of reproductive female and volant juvenile northern long-eared bats were located nearer to both woody

wetlands and upland forests than other cover types on the local landscape (De La Cruz et al. 2022a). Northern long-eared bats used riparian woody wetlands adjacent to upland pine-dominated evergreen forests at The Nature Conservancy's Piney Grove Preserve (PGP) in Sussex County, Virginia, as overwintering habitat (De La Cruz et al. 2022b). Although northern long-eared bats at the PGP were observed to roost in sweetgum, red maple, and tupelo, within or directly adjacent to woody wetlands, it may be that northern long-eared bats are actively selecting these sites due to proximity to pine stands. In Arkansas, northern long-eared bats were shown to prefer thinned, mature pine stands (Perry and Thill 2007). Additionally, research at the Kisatchie National Forest (KNF) on the upper Gulf Coastal Plain of Louisiana indicated that northern long-eared bats select pine as both summer and winter roosts (Garcia et al. 2023). Although northern long-eared bats largely overwintered in deciduous trees in the Croatan National Forest (CNF) on the Coastal Plain of North Carolina (Jordan 2020), the CNF contains a significant upland pine-dominated evergreen component. Minimally, our results support the conservation and management of a diverse mosaic of woody wetlands juxtaposed by upland forests, often characterized as pine-dominated evergreen forests. Beyond the simple association of this cover mosaic, it may be that northern long-eared bats use heterogenous forested areas created by active management such as prescribed fire. Intriguingly, the KNF, CNF, PGP, and Big Woods WMA are all dominated by a mosaic of woody wetland and pine-dominated evergreen forests, with upland pines often managed using prescribed fire (Watts and Harding 2007, Haywood 2012, Taillie et al. 2016). Specifically, we collected the greatest number of northern long-eared bat echolocation files at the Virginia Department of Wildlife Resources' Big Woods Wildlife Management Area (WMA), in Sussex County. Prescribed fire has been shown to enhance resource availability to northern long-eared bats at the intersection of cover types in other physiographic provinces (Johnson et al. 2009). It is possible that northern long-eared bats actively forage and roost proximal to the intersection of woody wetlands and upland forests, including fire-managed pines. Therefore, prescribed fire may be beneficial in promoting the continual formation of day-roosts and the variety of conditions needed for year-round use by this species in the region.

Northern long-eared bat activity was more likely to be documented in the non-winter than winter season, but total relative activity did not differ between seasons, supporting the observed year-round presence of northern long-eared bats in northeastern North Carolina and southeastern Virginia (Jordan 2020, De La Cruz et al. 2022b). Furthermore, while we observed that probable activity was highest between 10 and 25 C, we found no relationship between relative activity and temperature. Generally, bat

activity is limited by prey availability and the thermoregulatory demands of foraging in lower ambient temperatures (Bernard and McCracken 2017). However, on the Coastal Plain, warmer winter temperatures (Grider et al. 2016) and year-round insect availability (Jordan 2020) likely decrease the obstacles to winter foraging. Locally, Whitaker et al. (1997) observed that eastern red bats in the Great Dismal Swamp of North Carolina and Virginia successfully foraged on Diptera (i.e., true flies) and Lepidoptera (i.e., moths) during winter. Similarly, in eastern and central Tennessee, Bernard et al. (2021) observed that bats, including northern long-eared bats, also foraged on true flies and moths during winter. Because we observed no variation in relative activity in relation to season or temperature, it seems likely that prey is readily available to northern long-eared bats even during winter. Interestingly, our results indicate that probable activity was highest during non-winter seasons at temperatures between 10 and 25 C. The upper thermoneutral zone for bats of the family Vespertilionidae is 30 C (Patriquin et al. 2016), suggesting our findings highlight the optimal temperature range for recording northern long-eared bat activity in the region. Jordan (2020) documented that northern long-eared bats enter torpor during temperatures approaching freezing on the Coastal Plain of North Carolina. Northern long-eared bat activity in coastal areas of the southeastern U.S. may be more influenced by short-term thermoregulatory requirements (e.g., decreased movement during extreme hot or cold periods) than seasonal resource availability.

Although prey availability (Bernard and McCracken 2017) and extreme weather events (Grider et al. 2016) undoubtedly alter bat activity, peak probable activity related to temperature may also be linked to the reproductive phenology of northern long-eared bats in northeastern North Carolina and southeastern Virginia. For example, De La Cruz et al. (2022a) observed that early volancy of juvenile northern long-eared bats on the Coastal Plain of North Carolina was linked to the early onset of the growing season in the region. Thermally stable roosts during the early growing season likely allow maternity colonies to remain normothermic, accelerate fetal growth, and produce consistent lactation earlier in the year (Burrell and Bergeson 2022). These conditions may then allow for early parturition and volancy, providing juvenile northern long-eared bats an extended developmental period to accumulate fat stores prior to winter hibernation or extended torpor (Geluso et al. 2019). However, researchers have also observed use of short, decayed, and highly shaded roosts by post-lactating adults and volant pups, likely indicating the reduced thermal requirements of colonies post-volancy (Perry and Thill 2007, Patriquin et al. 2016, De La Cruz et al. 2022a). Previously, it was assumed that the addition of newly volant pups onto the landscape would result in a spike

of local acoustic activity (Ford et al. 2011). However, recent research indicates that for many species peak activity occurs during lactation rather than juvenile volancy (Deeley et al. 2022). Therefore, northern long-eared bat activity peaks prior to both juvenile volancy and the height of summer heat are likely coinciding with the high energy demands of lactation and the rearing of young. Furthermore, extreme weather events of coastal areas (Grider et al. 2016) may necessitate selection of contiguous tracts of woody wetlands and intersecting pine-dominated evergreen forests that provide adequate protection from inclement conditions during both maternity (Perry and Thill 2007, Patriquin et al. 2016) and non-maternity seasons (Jordan 2020).

Northern long-eared bats appear to be both reproductive and overwintering season residents of northeastern North Carolina (Jordan 2020) and southeastern Virginia (De La Cruz et al. 2022b). Despite documenting relatively consistent widespread northern long-eared bat activity, our highest call totals were localized to the Coastal Plain of Virginia and North Carolina. Additionally, call counts, particularly those collected during the spring and summer, may suggest that these areas contain multiple active northern long-eared bat maternity colonies (Ford et al. 2023). Future surveys to locate new reproductive populations of the species may benefit from targeting heterogenous forest sites, with emphasis on forest mosaics characterized by woody wetlands with associated upland pine-dominated evergreen forest, during warm (10–25 C) periods of non-winter seasons. Whereas northern long-eared bats require relatively large areas of contiguous woody wetlands and upland forests for both roosting and foraging on the Coastal Plain of North Carolina (Jordan 2020, De La Cruz et al. 2022a), the species also selects cover regularly subjected to small-scale disturbances that establish new roosts and improve conditions in existing roosts (Johnson et al. 2009, Ford et al. 2016). Specifically, northern long-eared bat activity appears to increase with increasing proportions of both woody wetlands and pine-dominated evergreen forests, possibly including pine stands managed using prescribed fire. Management of unique coastal cover, specifically a diverse mosaic of woody wetlands juxtaposed by upland forest and/or fire-managed pines, may provide habitat for both reproductively successful summer maternity colonies and overwintering populations of northern long-eared bats in the region. Our findings suggest that heterogenous coastal forests, specifically woody wetlands and associated upland pine stands, are likely important habitat for northern long-eared bats in the Mid-Atlantic. Implementing management strategies that maintain and enhance these unique habitats may support both maternity and overwintering population establishment of this endangered species.

Acknowledgments

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