

Ecology of northern long-eared bats (*Myotis septentrionalis*) in a coastal setting after the introduction of White-nose Syndrome

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Abstract

Northern long-eared bat (*Myotis septentrionalis*) populations have declined sharply in recent years due to the introduction and rapid spread of White-nose Syndrome. This has prompted an urgent need for a greater understanding of their natural history in order to support the conservation of extant populations, particularly where forested day-roost and foraging habitats are being fragmented by development. Prior to 2006, with other *Myotis* species on the endangered species list, northern long-eared bats were understudied. In recent years, with the pressing concern to document the ecology of all cave bats affected by White-nose Syndrome on the landscape, researchers have now prioritized northern long-eared bat habitat needs, day-roost use, social dynamics, and barriers to gene flow. A relatively new discovery has been the numerous coastal populations that occur in smaller forest patches often surrounded by anthropogenic development. The goal of my research is to aid in informing future monitoring and management protocols that are specific to northern long-eared bats, particularly as they may shift from Threatened to Endangered under the Endangered Species Act. The chapters of this dissertation explore (1) similarities and differences between coastal and more documented upland habitat associations for populations of northern long-eared bats throughout the summer months through the use of acoustic detectors; (2) relationships between acoustic activity patterns and weather on an hourly basis for several bat species on Long Island, New York; and (3–4) day-roost characteristics and social network dynamics of a coastal northern long-eared bat maternity colony on Long Island, New York. I found that northern long-eared bat colonies have larger spatial footprints in – and a moderate tolerance for – forests in anthropogenically-developed areas than previously believed, though many natural history aspects of the bat were similar among coastal and interior populations. Installation of artificial day-roost structures such as bat boxes would likely be used and highly beneficial to colonies in these conditions, particularly to offset the deleterious effects of stochastic disturbance events on day-roost availability and to support social cohesion (and, by extension, reproductive success) for coastal maternity colonies. Additionally, I found that acoustic activity increased in riparian areas, or at sites closer to water features, and as proportion of forest coverage increased at a broad scale. However, immediately around the detector this

relationship was reversed. Taken together, this demonstrates that riparian corridors, water features, and forest structural heterogeneity should explicitly be included in management guidelines.

Ecology of northern long-eared bats (*Myotis septentrionalis*) in a coastal setting after the introduction of White-nose Syndrome

Katherine Gorman
General Audience Abstract

White-nose Syndrome is a fungal disease that has killed millions of cave bats in North America, including the northern long-eared bat (*Myotis septentrionalis*) that during the spring through fall uses forests for roosting and foraging habitat. As the disease continues to spread, and as forests are increasingly being lost to urbanization, it is imperative for researchers and land managers to understand the landscape needs of this species so that they can retain those forests that are used by this species. In addition to broader landscape needs, it is important to understand what specific forest stand to tree features the bats are using, how their social dynamics support their reproductive success, and how to best support habitat conditions foster mating in the fall swarm to avoid inbreeding. In recent years, more northern long-eared bats have been documented in coastal landscapes, suggesting that these areas might be more important to the conservation of the species than previously believed. In this dissertation, my aim was to explore how or why the landscapes in these coastal areas were being used by these bats both during nightly foraging and during the day as resting areas (day-roosts). Additionally, I explored how multiple species of bats were responding to weather conditions on the coast across seasons. Overall, I found that complex forests continue to be an important resource for northern long-eared bats, as well as water features whereby the latter should be more explicitly included in conservation management plans. Northern long-eared bats also show an ability to successfully use small forest patches within a larger urbanized landscape, including using human structures for day-roosts. Human structures might provide reliable, multi-year day-roosts in areas where extreme coastal weather events (hurricanes) occur or increase or as natural processes reduce the suitability of these forests to provide day-roosts. These structures, particularly artificial roost boxes could also support the social network of reproductive northern long-eared bats and thus maintain population stability to some extent.

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Preface

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Introduction

White-nose syndrome (WNS) is a disease affecting bats that was first detected in upstate New York in the winter of 2006 (Blehert et al., 2009). It is caused by the fungal pathogen *Pseudogymnoascus destructans* (*Pd*) and has contributed to dramatic declines via direct mortality or reduced fitness in several cave-hibernating bat species as it spread across North America. As of October 2022, bats with WNS have been confirmed in eight Canadian provinces and 38 states, and *Pd* is suspected to be present in five additional states (White-Nose Syndrome Response Team, 2022; Figure 1). In areas affected, declines of some species, such as northern long-eared bats (*Myotis septentrionalis*), have exceeded 90% below pre-WNS populations (Cheng et al., 2021; Powers et al., 2015; Turner et al., 2011).

This population decline has led to the northern long-eared bat being listed as Threatened under the Endangered Species Act in 2015 (Department of the Interior: Fish and Wildlife Serv, 2015). Moreover, as of March 2022, this species has been proposed for reclassification to Endangered status (Bies, 2020; U.S. Fish and Wildlife Service, 2022). Although some WNS-affected species such as little brown bats (*Myotis lucifugus*) show some evidence of post-WNS stability and recovery (Dobony and Johnson, 2018), declining trends in northern long-eared bat populations have largely continued unabated in most regions. Researchers do not yet have a clear understanding about the larger ecological consequences of this decline, but given the critical role bats play in ecosystem services in the agricultural and forestry sectors, it is likely that the costs of these bat declines will be both biologically and economically significant and widespread (Frick et al., 2010; Jachowski et al., 2014; Kunz et al., 2011; Maine and Boyles, 2015).

Globally, acoustic sampling often is employed to describe seasonal bat community activity patterns, to elucidate habitat associations, and to document focal areas for mist-netting surveys (Ford et al., 2011). From a survey efficiency perspective, acoustic techniques have been shown to more quickly and completely tally species richness than mist-netting alone (Coleman et al., 2014; Murray et al., 1999). The use of acoustic samples is accepted by the U.S. Fish and Wildlife Service for use in presence/absence surveys for certain Endangered and Threatened bat species, including northern long-eared bats (U.S. Fish and Wildlife Service, 2015). Given the difficulty in mist-netting declining species such as the northern long-eared bat, researchers and managers will invariably transition to a greater dependence on acoustic surveys to determine bat presence and community assemblages, as well as tracking population indices (Reynolds et al., 2021; Robbins et al., 2008). Determining how to interpret the acoustic data (based on

call abundance/frequency or detector-to-detector variation) will be indispensable to critical management decisions regarding landscape and habitat use by bats at varying scales.

Though poorly quantified, regional weather and meteorological phenomena are known to trigger movements and activity levels of several species, including northern long-eared bats (Dechmann et al., 2017; Patriquin et al., 2016; Smith and McWilliams, 2016; Whitaker and Rissler, 1992). During the dormant season, northern long-eared bats will hibernate in relatively humid caves with year-round seasonal temperatures averaging between 2–14°C; this corresponds to the ideal growing temperatures for *Pd* spores (about 5–10°C, but up to 15°C, Blehert et al. 2009, Cryan et al. 2010). However, some persisting northern long-eared bats using non- or less-WNS-impacted hibernacula in the winter have been identified in coastal areas of the Northeast and mid-Atlantic (De La Cruz et al., 2020; Dowling and O’Dell, 2018; Grider et al., 2016). One such population resides on Long Island, New York. In theory, a shorter distance between summer foraging grounds and winter hibernacula exposed to less extreme temperatures could allow the bats to enter hibernation later and emerge earlier, while overwintering with little to no exposure to *Pd*. It is unclear as to whether coastal residence throughout the winter is a recent adaptive strategy for northern long-eared bats or if this phenomenon was present and unknown for years. If these coastal populations continue to endure, these alternative hibernacula could serve as a potential refugia and “life boat” for the species, a potential recolonization source for the interior, and a critical source for genetic diversity if a solution to WNS is found and applied.

With an overall propensity to choose cavities over bark and foliage as roost sites (Menzel et al., 2002), most studies show varied use of tree species depending on geographic locale (Carter and Feldhamer, 2005; Garroway and Broders, 2008; Lacki and Schwierjohann, 2001; Stein and White, 2016a; Timpone et al., 2010), stand-level ecological processes, and successional stage (Silvis et al., 2012). Small forested patches on Long Island that are serving as maternity staging grounds are vulnerable to stochastic, stand-replacing events such as hurricanes. A resulting loss in critical roosting habitat may be detrimental to an already-strained population, particularly one of the few remaining and reproductively-successful colonies that have been accounted for in recent years (Kalen et al., 2022; Reynolds et al., 2016).

The presence of fission–fusion dynamics of bat social groups has been documented for several species, including northern long-eared bats prior to WNS. Fission–fusion societies are characterized by a communal use of one to two primary roosts, or nodes (fusion). Bats will then periodically leave these primary roosts to use multiple secondary roosts either alone or with one to two other bats (fission). Though poorly studied in cave bats in North America, observations of fission–fusion dynamics among Indiana bats (*Myotis sodalis*; Silvis et al., 2014b) and reproductive female northern long-eared bats has

begun to be documented in recent years (Ford et al., 2016; Johnson et al., 2012; Silvis et al., 2015, 2014b, 2014a). Researchers have confirmed that maternity colonies of northern long-eared bats are highly social and form non-random associations between individuals. It is hypothesized that the locational or structural characteristics of chosen roosts might be influenced by reproductive status (and thus thermoregulatory needs) of females (Garroway and Broders, 2008; Stein and White, 2016a).

However, as of yet, no maternity roost social networks post-WNS have been observed in detail or over multiple years, with several studies finding these bats roosting alone or in pairs rather than an organized colony (Thalke and Lacki 2018, S. Deeley and S. Freeze, Virginia Polytechnic Institute and State University, pers. comm.). Any overlap or recurring patterns that add to our knowledge of bat social networks or roost requirements could aid ongoing conservation and recovery actions in the east and possibly aid in the development of western conservation strategies (Carter and Feldhamer, 2005; Stein and White, 2016).

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Figures

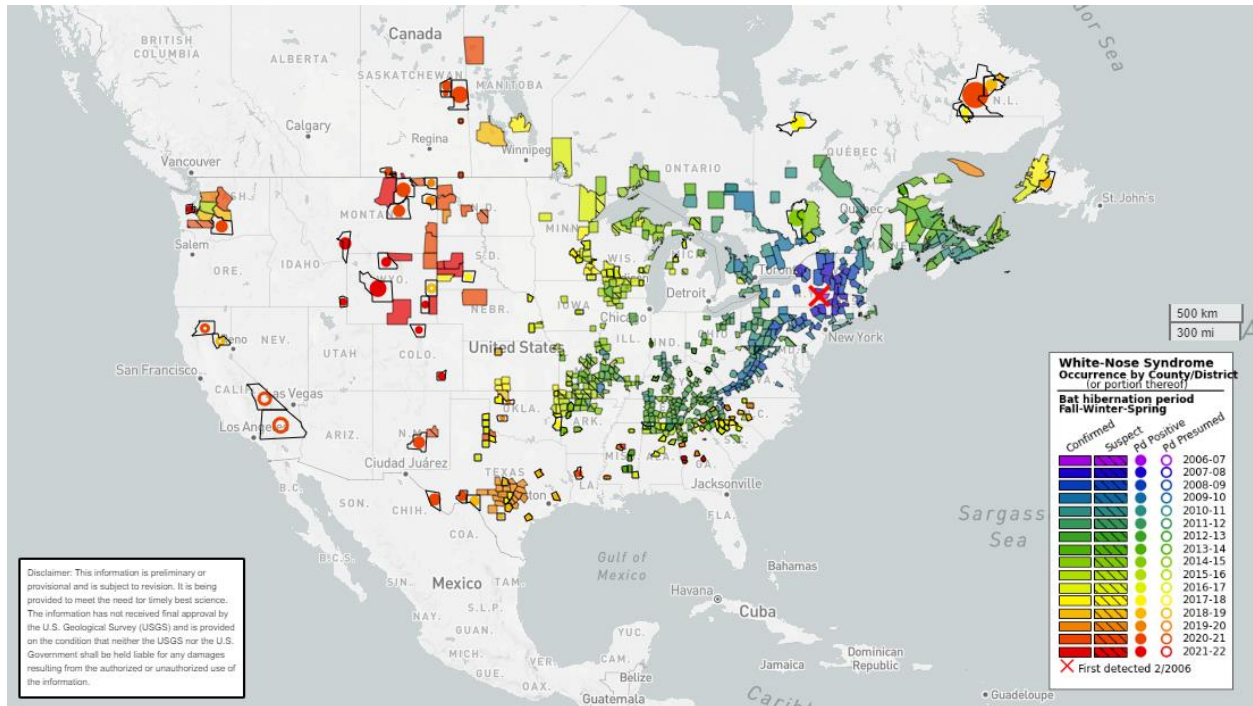


Figure 1. White-nose syndrome occurrence map (as of October 2022) from White-Nose Syndrome Response Team (2022).

Broad-scale geographic and temporal assessment of northern long-eared bat maternity colony landscape association

Abstract

As the federally threatened northern long-eared bat (*Myotis septentrionalis*) continues to decline due to White-nose Syndrome (WNS) impacts, the application of effective conservation measures are needed but often hindered by the lack of ecological data. To date, recommended management practices have been adopted in part from other federally listed sympatric species such as the endangered Indiana bat (*M. sodalis*). During the maternity season, these measures have largely focused on conservation of known day-roost habitat, often with little consideration for foraging habitat, particularly riparian areas. We examined acoustic activity of northern long-eared bats relative to day-roost and capture data at coastal and interior sites in the District of Columbia, New York, Pennsylvania, Virginia, and West Virginia, USA, over the course of 6 summers (2015–2020), where maternity activity was still documented after the initial arrival and spread of WNS. Acoustic activity of northern long-eared bats relative to forest cover decreased at the acoustic site level (fine scale) but increased at the sampling region level (coarse scale). We observed a positive association of northern long-eared bat acoustic activity with riparian areas. Additionally, we observed higher levels of activity during pregnancy through early lactation period of the reproductive cycle prior to juvenile volancy. Our findings suggest the need for more explicit inclusion of forested riparian habitats in northern long-eared bat conservation planning. Acoustic sampling in spring and early summer rather than mid- to late summer and in forested riparian areas are the most effective strategies for identifying potential active northern long-eared bat maternity colonies on the local landscape.

Introduction

Understanding the ecological relationships of bats to their environment is a critical first step in developing effective management plans for their conservation (Henderson et al., 2008; Rodríguez-San Pedro and Simonetti, 2015; Threlfall et al., 2012). The northern long-eared bat (*Myotis septentrionalis*) is a summer, forest day-roosting obligate bat that typically hibernates in caves or mines (and other such environments) in the winter (Caceres and Barclay, 2000). They have been severely impacted by White-

nose Syndrome (WNS; Broders et al., 2006; Silvis et al., 2016) and, as a result of precipitous declines, this species has been listed as Threatened under the Endangered Species Act (ESA) since 2015 (U.S. Fish and Wildlife Service, 2015a). It currently is undergoing an additional assessment for possible up-listing to Endangered in the United States (Bies, 2020). Additionally, some colonies are showing declining or failed recruitment (Francl et al., 2012; Reynolds et al., 2016), further inhibiting the stability or growth of the remaining populations.

Female northern long-eared bats form maternity colonies in forests during the spring and summer that integrate multiple day-roosts in trees and snags into a multi-node network within a discrete area (B. Hyzy et al., 2020; Silvis et al., 2016). Due to large population declines from WNS impacts, documenting northern long-eared bat presence via mist-netting has become more difficult (Reynolds et al., 2016). Accordingly, acoustic detection now plays a key role determining northern long-eared bat presence across the landscape (Barr et al., 2021; Francl et al., 2012). Despite population declines throughout much of their range, researchers have found several northern long-eared bat populations overwintering in coastal areas far removed from their traditional karst/mine hibernacula (Brown et al., 2007; Dowling and O'Dell, 2018; Jordan, 2020), as well as a few residual populations in interior regions similarly distant (De La Cruz et al., 2018). Understanding activity patterns related to reproductive periods is necessary for developing monitoring approaches. After parturition, juveniles remain non-volant for about three weeks (Krochmal and Sparks, 2007); when they enter the landscape, foraging patterns may shift within the population, which may indicate a need to reassess monitoring tactics. This conclusion was confirmed by Adams (1997), who noted differences in foraging patterns between juveniles and adult little brown bats (*M. lucifugus*), a sympatric species.

The range of northern long-eared bats encompasses nearly the entire eastern United States (excluding much of the South) and across much of Canada. As a clutter-adapted, forest-obligate species, it is assumed that higher levels of northern long-eared bat acoustic activity occur in more densely forested regions. This assumption is based on these areas having more complex forest composition and structure (variety in canopy cover, gaps, and height in addition to larger, unbroken tracts of day-roosting habitat), topography (elevational gains and losses), and less urbanization (Ford et al., 2005; Johnson et al., 2008). Clutter is widely used to describe forest areas with high vegetative density and structural complexity (O'Keefe et al., 2014).

However, in recent years, maternity colonies have been found in more developed coastal areas (Gorman et al., 2021; Jordan, 2020) as opposed to the denser forests that typically constitute their habitat. After the population decline brought on by WNS, these residual coastal populations in more urban areas, as well as remaining, inland counterparts in forests (De La Cruz et al., 2018; Thalken et al., 2018), represent an opportunity to evaluate relative use of different habitats. Prior to the onset of WNS, when the

species was widespread and common, a detailed description of habitat requirements was not a pressing concern (Silvis et al., 2016).

The operative 4(d) rule of the United States ESA (U.S. Fish and Wildlife Service, 2015a) applied to the northern long-eared bat is primarily focused on forest stand preservation and the prevention of the disruption of day-roosting habitat during the maternity season. Currently, the rule provides no consideration of forested riparian areas as foraging habitat, unless those habitat types fall within 50 m of a known roost tree (Ford et al., 2016; U.S. Fish and Wildlife Service, 2015a). Nonetheless, the USFWS has created guidance intended to maximize detection of acoustic recordings of northern long-eared bats on the landscape that includes monitoring riparian corridors in addition to forest and forest-edge habitats (U.S. Fish and Wildlife Service, 2015b). Previous studies focused specifically on roost- or stand-level characteristics of female northern long-eared bat habitats have been limited in geographic scope (constrained to 1 study area at a time) and have placed limited attention on water resources as a roosting habitat feature (Garroway and Broders, 2008; Owen et al., 2003; Pauli et al., 2015; Thalken et al., 2018).

Herein, our aim was to determine the temporal and environmental parameters that influence northern long-eared bat acoustic activity in proximity to maternity colony areas. We used data collected from 7 independent research projects in the mid-Atlantic USA ranging from developed coastal sampling regions to interior forested mountain sampling regions. Rather than examining forest coverage as a single encompassing habitat component, our goal was to explore forest coverage effects on activity levels at fine and broad scales. We hypothesized that a higher percentage of forest cover at the broad scale would result in higher levels of activity due to increased roost availability and prey diversity (Ober and Hayes, 2008). Additionally, due to the larger number of female northern long-eared bats we captured in coastal areas, we predicted those sampling regions would have higher levels of northern long-eared bat acoustic activity regardless of forest coverage.

Materials and methods

Sampling regions

Our study area included seven mid-Atlantic sampling regions where we documented reproductive female or juvenile northern long-eared bats (Figure 0-1). We classified sampling regions located in the Coastal Plain or the Fall Line boundary with the Piedmont as ‘coastal’ and Appalachian Mountains or upper Piedmont sampling regions as ‘interior’. The Coastal Plain is largely urbanized with fragmented

forest patches and is bordered by the ocean to the east. The Appalachian Mountains to the west provide a stark contrast, with large swaths of contiguous forest, open agricultural land, and karst landscapes.

We classified three units in this study as falling within the coastal region. Completely surrounded by urban/suburban development and the Atlantic Ocean, the 248 ha William Floyd Estate (WIFL) portion of National Park Service (NPS) Fire Island National Seashore in New York is located in the Atlantic Coastal Plain physiographic province and composed of open fields, salt marsh, and unmanaged northern maritime forest that includes red maple (*Acer rubrum*), pitch pine (*Pinus pungens*), black locust (*Robinia pseudo acacia*), oaks (*Quercus* spp.), and sassafras (*Sassafras albidum*; Klopfer et al., 2002). The 710 ha NPS Rock Creek Park (ROCR) in Washington, DC, and 28 500 ha Marine Corps Base Quantico/NPS Prince William Forest Park (PRWI) complex in Virginia are located along the Fall Line boundary between the lower Piedmont and the Atlantic Coastal Plain. Forests at ROCR and PRWI are dominated by hickories (*Carya* spp.), oaks, and maples; additionally, there are stands of Virginia (*P. virginiana*) and loblolly (*P. taeda*) pine (the latter being limited to PRWI). The PRWI complex features numerous open fields used for military training, and forest management practices such as harvesting and prescribed burning occur regularly (Deeley, 2019).

Four additional units make up the interior region used in this analysis. The 2340 ha NPS Gettysburg National Military Park (GETT) is located in the upper Piedmont physiographic province east of the Blue Ridge Mountains. Landcover at GETT consists of a mixture of open fields and scattered, mature woodlots dominated by oak-hickory, red maple, and yellow poplar (*Liriodendron tulipifera*). The 79 900 ha NPS Shenandoah National Park (SHEN) in Virginia, the 3221 ha Back Creek Mountain (BCMT) portion of the George Washington National Forest in Virginia, and the 1153 ha West Virginia Division of Natural Resources' Jug Wildlife Management Area (TJUG) in West Virginia occur in the Blue Ridge, Ridge and Valley, and western Allegheny Plateau portions, respectively, of the Appalachian Mountains physiographic province, each with complex mountain topography and wide variation in elevation. These three sampling regions are almost completely forested with predominately oak-hickory, mixed mesophytic and xeric mixed oak-pine types, along with montane riparian areas dominated by white pine (*P. strobus*) and eastern hemlock (*Tsuga canadensis*). Forests at SHEN and TJUG are largely unmanaged, whereas portions of BCMT include large prescribed burn and regeneration units. SHEN, however, does have a long history of large wildfire events that have altered forest structure and composition relative to bat habitat (Austin et al., 2020).

Field methods

From 2015 to 2019 (15 May–15 August), we captured bats using single-, double-, and triple-high mist nets set over streams, and along forested trails and woodland roads used as flyways for bats (Deeley, 2019; Silvis et al., 2012). Demographic data were recorded for all bats captured, which included species, sex, and age class (adult or juvenile; Brunet-Rossinni and Wilkinson, 2009). Adult female northern long-eared bats and juveniles of both sexes weighing >5.4 g were outfitted with a 0.27 g Holohil LB-2X radio-transmitter (Holohil Systems) affixed between the scapulae using Perma-Type surgical cement (Perma-Type Company; Silvis et al., 2014). We used TRX-1000S receivers and folding 3-element Yagi antennas (Wildlife Materials) to track bats to day-roosts (Silvis et al., 2012). Roost locations identified through radio-tracking (as well as net capture sites) were georeferenced using handheld GPS units (Garmin). We used all locations where female or juvenile northern long-eared bats were documented (capture sites and roosts) in our analysis. Handling of bats occurred under the auspices of the Virginia Polytechnic Institute and State University's Institutional Animal Care and Use Committee protocols 16-240 and 19-227 and appropriate state and federal permits.

Capture and acoustic monitoring sites were chosen based on individual project needs, ranging from targeted northern long-eared bat research (day-roost surveys and descriptions) to general bat monitoring of multiple species (Austin et al., 2018, 2020; Barr et al., 2021; Deeley et al., 2021; Ford et al., 2005). At most sampling regions, acoustic recording occurred the same year(s) as mist-netting efforts (Table 0-1). Songmeter-ZC and SM4BAT ZC (Wildlife Acoustics) zero-crossing bat detectors with SMM-U1 omni-directional microphones were deployed at all sites. We located acoustic sites along streams, wetland edges, interior forest canopy gaps, forested trails, and single-track woodland roads. We attached detectors to trees with microphones mounted on 3–4 m high telescoping poles at least 3 m from the bole, except at SHEN, where microphones were attached directly to detectors to avoid microphone pole disturbance by American black bears (*Ursus americanus*). We programmed detectors to begin recording at least 30 min prior to local sunset and end recording at least 30 min after local sunrise.

Data preparation

To represent potential foraging areas, we created 2 km buffers in ArcGIS Pro (version 2.5.0, ESRI) around each northern long-eared bat day-roost or capture observation (Broders et al., 2006; Silvis et al., 2016). We then dissolved and merged all buffers at individual sampling regions to create polygons representing foraging and roost presence areas. We used data from acoustic sites that fell within these presence area polygons in our analysis (Figure 0-2 & Figure 0-3). To classify land cover at fine-scale

acoustic sites, we created a 30 m individual buffer around each acoustic site point, approximating the maximum effective detection distance for microphones (Agranat, 2014). We identified echolocation calls with Kaleidoscope Pro (Wildlife Acoustics; version 5.2.1; Classifier version 5.1.0; 0 Sensitivity Setting) following USFWS acoustic monitoring protocols required for documenting northern long-eared bat presence (U.S. Fish and Wildlife Service, 2017). However, we set a minimum threshold of three pulses per call file (as opposed to the two pulses used by the USFWS) to minimize bat species misclassification (Muthersbaugh et al., 2019), and only used nights with a maximum likelihood estimate value of high confidence (<0.05) for northern long-eared bats. We aggregated calls into nightly totals for analysis.

Following USFWS acoustic monitoring guidelines to optimize sampling and minimize false negatives (U.S. Fish and Wildlife Service, 2017), we only included nights without precipitation using weather data from Aviation Routine Weather Reports (Iowa State University, 2022). We combined three National Land Cover Dataset (NLCD; U.S. Geological Survey, 2019) forest land cover types: deciduous forest, evergreen forest, and mixed forest into one forest layer and used the Tabulate Area tool in ArcGIS Pro to calculate the proportion of forest within each presence area polygon, as well as each 30 m acoustic site buffer. If an acoustic site was placed within 30 m of either a hydrological unit (streams, rivers, swamp/marsh, or open water) from the US Geological Survey (USGS) National Hydrography Dataset (U.S. Geological Survey, 2020) or NLCD wetland/open water (U.S. Geological Survey, 2019), we categorized that site as riparian (Ford et al., 2005); this classification was also confirmed from acoustic deployment notes. We used the Near tool in ArcGIS Pro to calculate the distance (km) from each acoustic site to the closest northern long-eared bat capture or roost site.

Statistical analysis

We performed all statistical tests and analyses using R version 4.0.3 (R Core Team, 2020). We examined trends in nightly call totals to estimate pre- and post-volancy periods using the ggplot2 package (Wickham, 2016; Figure 0-4) to overlay all nightly activity from each acoustic site at each sampling region. We identified 2 distinct peaks in northern long-eared bat acoustic activity. The peak at the beginning of the acoustic sampling period likely reflects adult females establishing maternity colonies (Deeley et al., 2021). The decline in mid-June likely corresponds to parturition, with the increase in activity at the end of June until July corresponding to juvenile volancy and foraging followed by a gradual dispersal of bats from the natal area (Deeley et al., 2021; Ford et al., 2011; Rydell, 1993). Using this information, we approximated a general juvenile volancy start date at the low point between the two peaks in activity on June 24 (day of the year: 176; Deeley et al., 2021). Our capture results supported this

estimate, as all adult females were either pregnant or lactating prior to this date, and all juveniles were captured after this date.

We tested for collinearity among our predictor variables using Pearson's correlation coefficient in the `corrplot` package (Wei and Simko, 2021) and found no correlation $\geq |0.6|$ between predictors and therefore retained all variables for analysis. We performed a Shapiro-Wilk test for normality (R Core Team, 2020) and found that the response variable (total nightly calls at each acoustic site) was not normally distributed ($p < 0.001$). Therefore, we modeled acoustic activity of northern long-eared bats using a zero-inflated, negative binomial generalized linear mixed model (GLMM) with the `glmmTMB` package in R (Brooks et al., 2017). We created a set of 21 *a priori* candidate models (including a null model) using combinations of riparian/non-riparian designation, distance to nearest northern long-eared bat capture site or day-roost, pre-/post-juvenile volancy, region (interior or coastal), proportion of forest within presence area polygons, and proportion of forest within acoustic site range as independent variables, and acoustic site as a random variable. We included all covariates together, separately, and created a set of additional models using two to five covariates based on our ecological understanding of northern long-eared bats and their use of riparian habitat (Ford et al., 2005; Owen et al., 2003; Silvis et al., 2016). We parameterized the logistic portion of the zero-inflated models using the same covariates as the GLMM. We ranked each model using Akaike's information criteria (AIC; Burnham and Anderson, 2002) and considered all models within $\Delta\text{AIC} < 2$ to be potentially informative (Burnham and Anderson, 2002). We checked each model for goodness-of-fit and over- and under-dispersion in the form of a QQ plot, residual plot, and a 1-sample Kolmogorov-Smirnov test using the `DHARMA` package (Hartig, 2020).

Results

At our coastal sampling regions, we delineated presence area polygons ranging from 2133 to 5750 ha (Table 0-1). At our interior sampling regions, we delineated presence polygons ranging from 1911 to 3319 ha (Table 0-1). Our top model explaining northern long-eared bat activity included: distance to nearest net or day-roost site, riparian or non-riparian acoustic site, reproductive period, proportion of presence area forested, proportion of immediate acoustic site forested, and acoustic site as a random effect variable (Table 0-2). The second ranked model was the global model that included region (coastal vs. interior) that was not statistically significant ($p < 0.20$), so we considered the more parsimonious and hence the best-approximating model to be the first one.

Northern long-eared bat acoustic activity was higher throughout the pre-volancy period ($p < 0.001$; Table 0-3, Figure 0-5). Overall, activity increased with proportion of forest cover within the

presence area ($p = 0.010$) but decreased with proportion of forest cover within 30 m of the acoustic site ($p < 0.001$;). Detectors at riparian acoustic sites recorded higher levels of activity than at non-riparian locations ($x = 36 \pm 161$ vs. $x = 8 \pm 14$ call files [\pm SD], respectively, $p < 0.001$; Figure 0-7). Acoustic activity increased with increasing distance from known roost or capture site ($p < 0.001$; Figure 0-8).

Discussion

Although we predicted that acoustic activity would generally be greater in coastal areas than interior sampling regions, region was not statistically significant. The lack of difference in activity between interior and coastal areas suggests that inherent differences in landscape-scale habitat may not be the driving factor explaining the higher incidences of residual populations in coastal areas. Rather, resilience of extant coastal populations could be due to their ability to overwinter successfully outside of traditional hibernacula, potentially near these coastal maternity areas, and thus avoid exposure to WNS and minimize biological costs associated with longer spring and fall migratory movements as suggested in other studies (Dowling and O'Dell, 2018).

The USFWS considers the northern long-eared bat a forest-dwelling and clutter-adapted foraging specialist species (Carter and Feldhamer, 2005; Silvis et al., 2016; U.S. Fish and Wildlife Service, 2015a), largely emphasizing the importance of forest retention as a conservation strategy (Russo and Jones, 2003). Barr et al. (2021) observed that broad land cover types are useful in predicting northern long-eared bat presence on the landscape. Our results support this conclusion in part, as detection increased with forest coverage at a broad (presence area) extent. However, detection decreased with forest coverage at the acoustic site level, indicating that forest extent alone may not be an adequate descriptor of habitat quality. Although northern long-eared bats are able to forage in dense, upland forests, heterogeneity in forest coverage and condition (having dense forests interspersed with open areas) may support increased northern long-eared bat acoustic activity. More local and landscape forest heterogeneity invariably provides a wider diversity and timing of prey availability (Ober and Hayes, 2008), may facilitate inter-patch commuting, and provides a wider range of day-roosts (Silvis et al., 2016).

Our results indicate that riparian areas maintain ecological importance to northern long-eared bat activity; it is likely that upland forest alone does not satisfy their habitat requirements, despite previous acoustic studies having a large focus on forest coverage as the most important indicator of northern long-eared bat habitat (Ford et al., 2005; B. A. Hyzy et al., 2020; Thalken et al., 2018). Riparian areas have greater insect prey bases or availability for bats as well as providing sources of water, which could be critical when female bats are pregnant or lactating (Ober and Hayes, 2008; Russo and Jones, 2003;

Vaughan et al., 1997). Additionally, riparian areas, particularly forested ones, facilitate movements between forest patches particularly in fragmented landscapes (Perry et al., 2008; Thalken et al., 2018).

Somewhat contrary to our expectations, detectors at acoustic sites in closest proximity to northern long-eared bat roost and capture sites recorded less activity than those further away but still within our assumed presence area polygons. Based on the short distances from original capture to day-roosts in some northern long-eared bat studies (Johnson et al., 2009; Silvis et al., 2012), assumptions about foraging activity and roost proximity may be highly site-specific. In West Virginia, Owen et al. (2003) observed northern long-eared bats selecting thinned forest stands for foraging, but Menzel et al. (2002) found them selecting more intact, unmanaged stands for roost sites within an overall foraging and roosting home range area. Our results suggest that acoustic sites near roost and capture sites possibly are more associated with brief commuting behavior (i.e., fewer call files), whereas more distant sites are associated with foraging areas and higher levels of commuting (i.e., many call files; Russo and Jones, 2003; Vaughan et al., 1997), perhaps due to the wide variability of forest condition within and among all of our study regions. As a result, the importance of an acoustic site with lower numbers of northern long-eared bat call files should not be diminished, particularly when surrounded by sites with higher levels of recorded activity.

We propose that management activities for northern long-eared bat conservation (in the form of forest stand management or the addition of artificial roosting structures) should not focus exclusively on upland forests, but rather consider forested riparian habitats and overall heterogeneity within forested stands and landscapes. Nonetheless, further research is needed to better assess both roosting and foraging habitat condition and spatial arrangement to determine how these two factors interact to drive overall habitat use by northern long-eared bats. Unfortunately, opportunities to do so, especially in the bulk of the species' distribution, will be difficult to accomplish in light of declines from WNS.

Literature cited

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Tables

Table 0-1. Total number of adult female and juvenile northern long-eared bats (*Myotis septentrionalis*) caught by survey sites, timeframes of acoustic data used in analysis, size of calculated presence area, number of acoustic sites used in analysis, total number of detector nights used in analysis, and mean \pm SD of nightly call files, 2015–2020.

Site	Location designation	No. of bats	Years (mist-netting)	Years (acoustics)	Estimated presence area (ha)	No. of acoustic sites	Detector nights	Mean nightly calls
Back Creek Mountain, Virginia	Interior	19	2015–2016	2015	3319	15	270	0.04 \pm 0.21
Gettysburg National Military Park, Pennsylvania	Interior	6	2018–2019	2018–2019	1663	5	576	0.13 \pm 0.64
The Jug Wildlife Management Refuge, West Virginia	Interior	6	2017	2017	1911	3	242	6.76 \pm 13.31
Shenandoah National Park, Virginia	Interior	7	2015–2016, 2018	2019–2020	1757	4	137	6.82 \pm 12.58
Marine Corps Base Quantico/ Prince William Forest Park	Coastal	6	2016–2017, 2019	2016–2017, 2019	5750	31	1939	0.19 \pm 0.83
Rock Creek Park, District of Columbia	Coastal	22	2016–2018	2016–2018	3758	20	699	1.68 \pm 6.35
William Floyd Estate, New York	Coastal	26	2018–2019	2018–2020	2133	19	2997	4.19 \pm 56.21

Table 0-2. Top 10 models relating northern long-eared bat (*Myotis septentrionalis*) to habitat variable, corresponding Akaike's information criterion (AIC) units, delta AIC units, and weights (ω_i). Dist.km: distance from acoustic site to nearest capture or roost site (2015–2019); riparian: binary category (riparian or dry site); volancy: binary (pre- or post-juvenile volancy date); proportion PA forested: proportion of presence area which was classified as forest; acoustic site forest: proportion of forest within 30 m of individual acoustic sites; region: binary variable (coastal or interior); (1|site): acoustic site as a random variable. Null model ranked lowest (highest AIC).

Model	AIC	Δ AIC	ω_i
Dist.km + riparian + volancy + proportion PA forested + acoustic site forest + (1 site)	7222.10	0.00	0.599
Dist.km + riparian + volancy + proportion PA forested + region + acoustic site forest + (1 site)	7223.30	1.20	0.329
Dist.km + riparian + volancy + acoustic site forest + (1 site)	7227.52	5.41	0.040
Dist.km + riparian + volancy + region + acoustic site forest + (1 site)	7228.41	6.31	0.026
Riparian + volancy + proportion PA forested + region + acoustic site forest + (1 site)	7231.17	9.06	0.006
Dist.km + volancy + proportion PA forested + region + acoustic site forest + (1 site)	7239.35	17.24	<0.001
Dist.km \times volancy + (1 site)	7253.51	31.41	<0.001
Dist.km + riparian + volancy + proportion PA forested + region + (1 site)	7256.78	34.68	<0.001
Dist.km + riparian + proportion PA forested + region + acoustic site forest + (1 site)	7257.53	35.43	<0.001
Dist.km + riparian + volancy + acoustic site forest + (1 site)	7261.25	39.15	<0.001

Table 0-3. Predictors, β -values, SE, z-values, p-values, and lower (LCL) and upper (UCL) confidence intervals for top model output of northern long-eared bat (*Myotis septentrionalis*) activity with habitat variables. Dist.km: distance from acoustic site to nearest capture or roost site (2015–2019); riparian: binary category (riparian or dry site); volancy (pre): binary (pre- or post-juvenile volancy date); proportion PA forested: proportion of presence area which was classified as forest; and proportion acoustic site forested: proportion of forest within 30 m of individual acoustic sites. Significant p-values (at the 0.01 confidence level) are shown in **bold**.

Zero-inflated model	β	SE	z	p	LCL	UCL
(Intercept)	-3.71	0.98	-3.79	< 0.001	-5.64	-1.79
Dist.km	0.97	0.25	3.84	< 0.001	0.48	1.47
Riparian	3.45	0.90	3.84	< 0.001	1.69	5.22
Volancy (pre)	1.31	0.29	4.60	< 0.001	0.75	1.87
Proportion PA forested	2.57	1.00	2.56	0.010	0.60	4.53
Proportion acoustic site forested	-3.46	0.77	-4.48	< 0.001	-4.98	-1.95

Figures

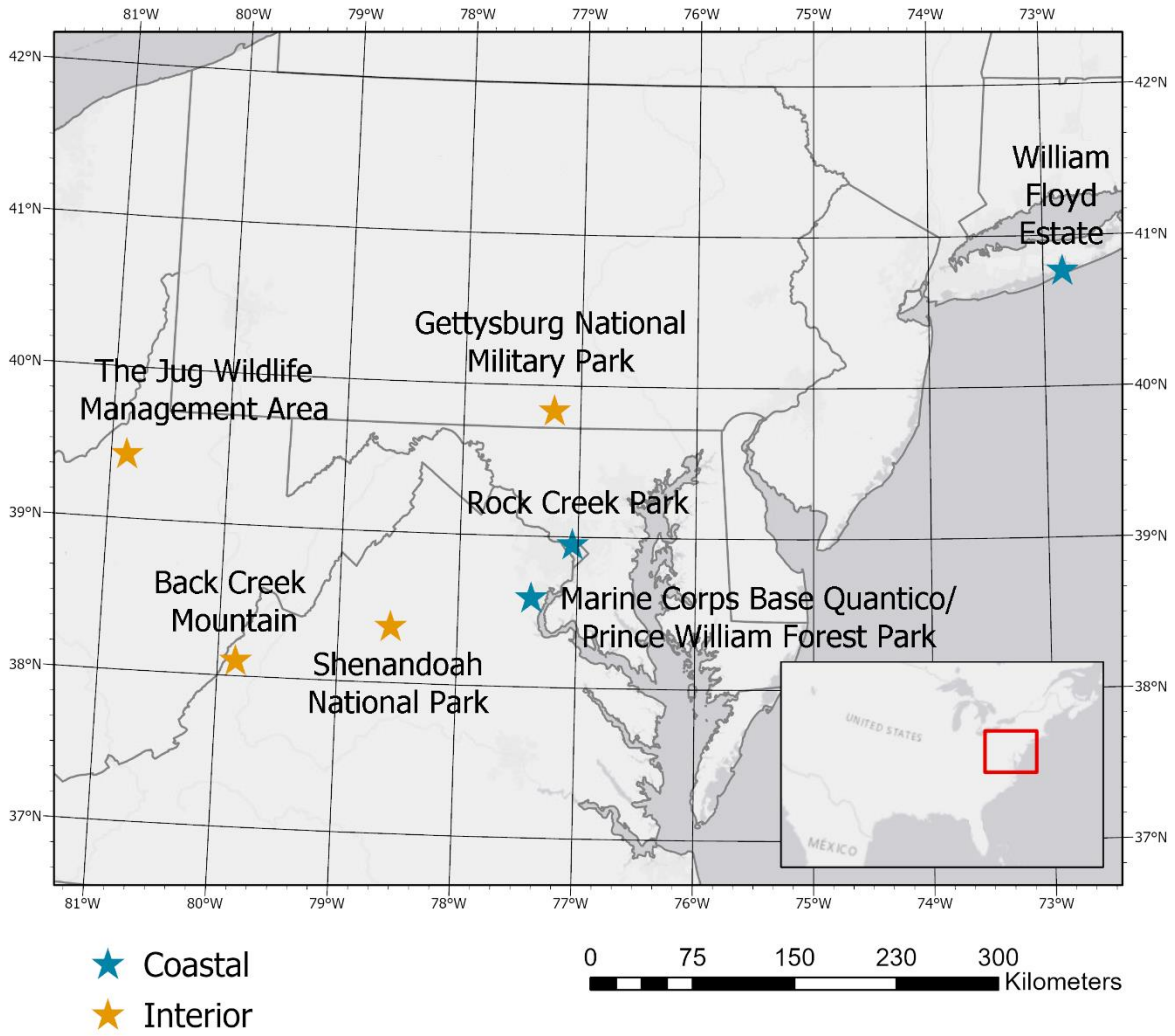


Figure 0-1. Coastal and interior northern long-eared bat (*Myotis septentrionalis*) sampling regions (2015–2020).

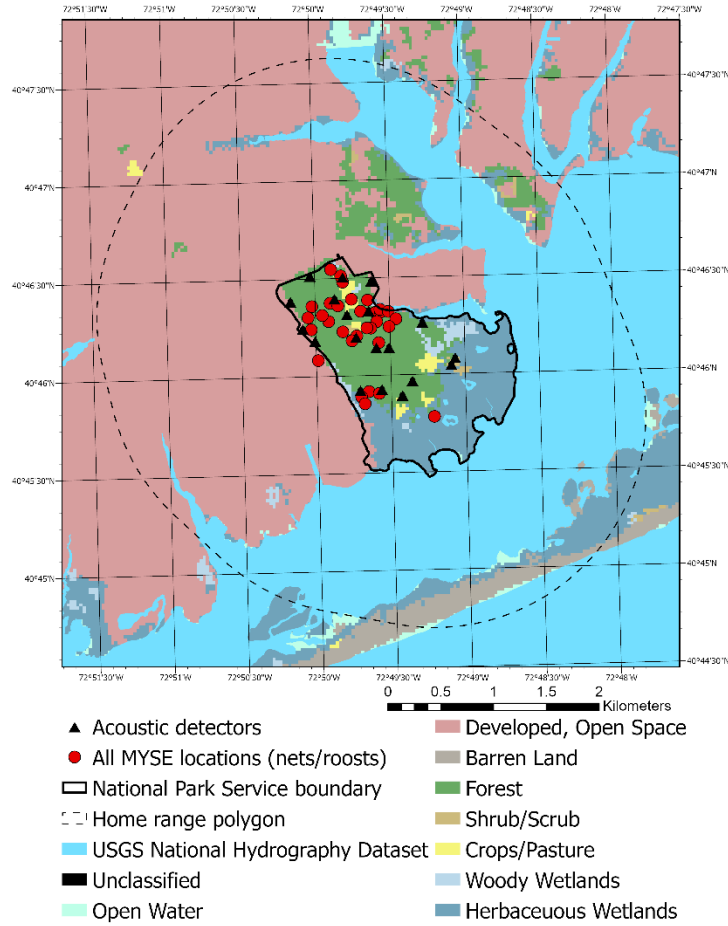


Figure 0-2. Example of a coastal sampling region showing capture and day-roost sites of northern long-eared bats (*Myotis septentrionalis*; all MYSE locations) and acoustic sites used in analysis on William Floyd Estate, Fire Island National Seashore, New York (2018–2020). Map shows broad land cover category and estimated bat presence area polygon (home range polygon).

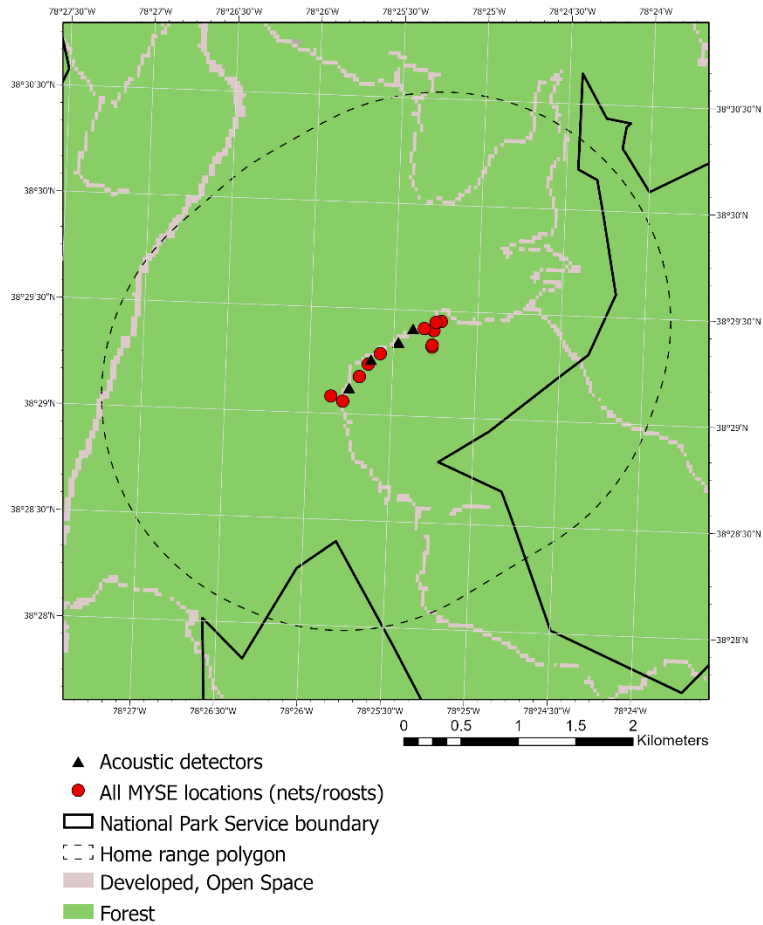


Figure 0-3. Example of an interior sampling region showing capture and day-roost sites of northern long-eared bats (*Myotis septentrionalis*; all MYSE locations) and acoustic sites used in analysis at Shenandoah National Park, Virginia (2015–2016, 2018). Map shows broad land cover category and estimated bat presence area polygon (home range polygon).

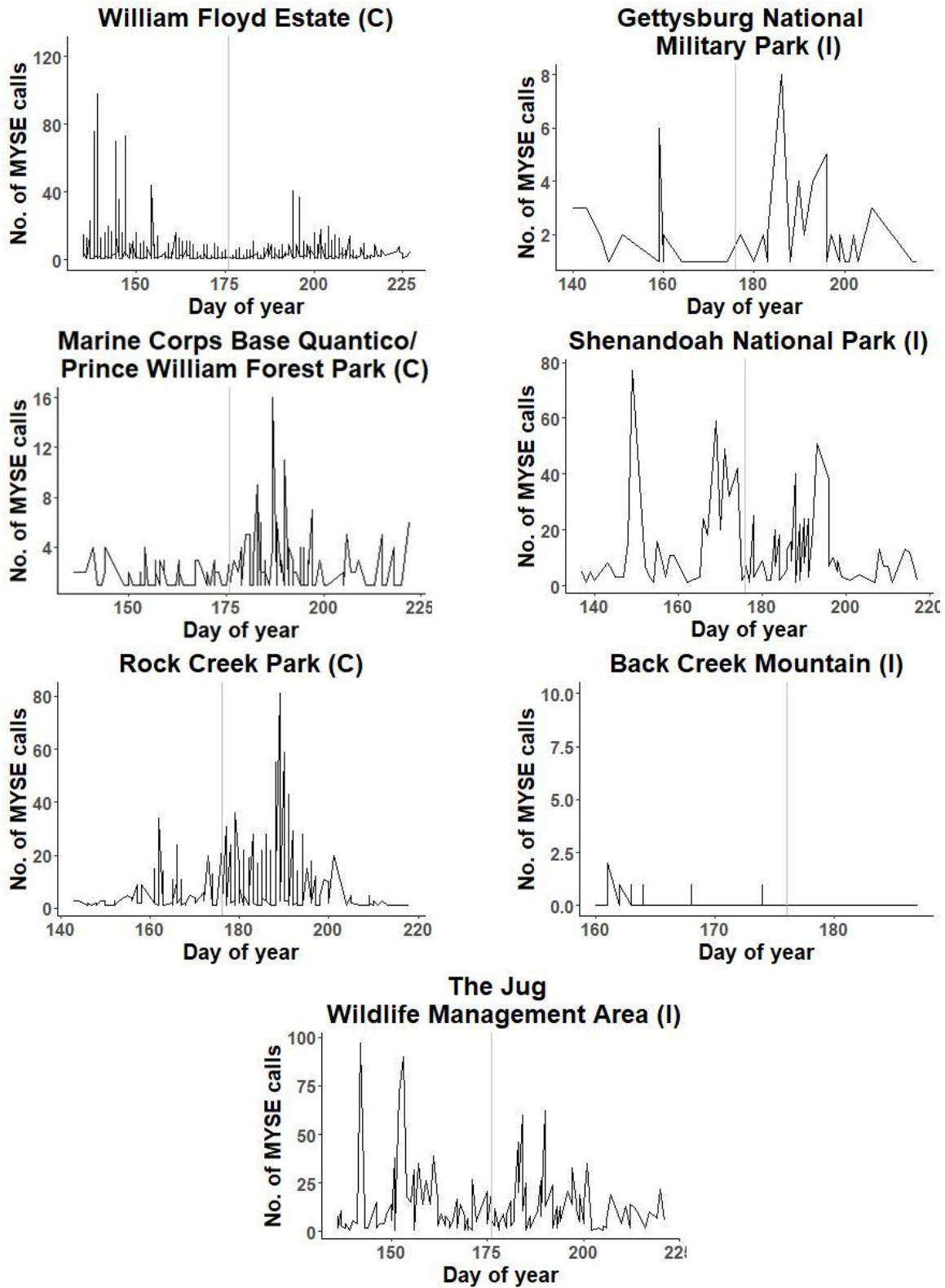


Figure 0-4. Total northern long-eared bat (*Myotis septentrionalis* [MYSE]) nightly calls during analysis period (May 15–August 15) at coastal (C) and interior (I) sampling regions. William Floyd Estate y-axis adjusted for visibility, cutting off 7 points before day of year 150. No. of MYSE calls: total number of northern long-eared bat call files per night; vertical gray lines: distinction between pre- and post-volancy dates. See Table 0-1 for timeframes of data used at each survey site.

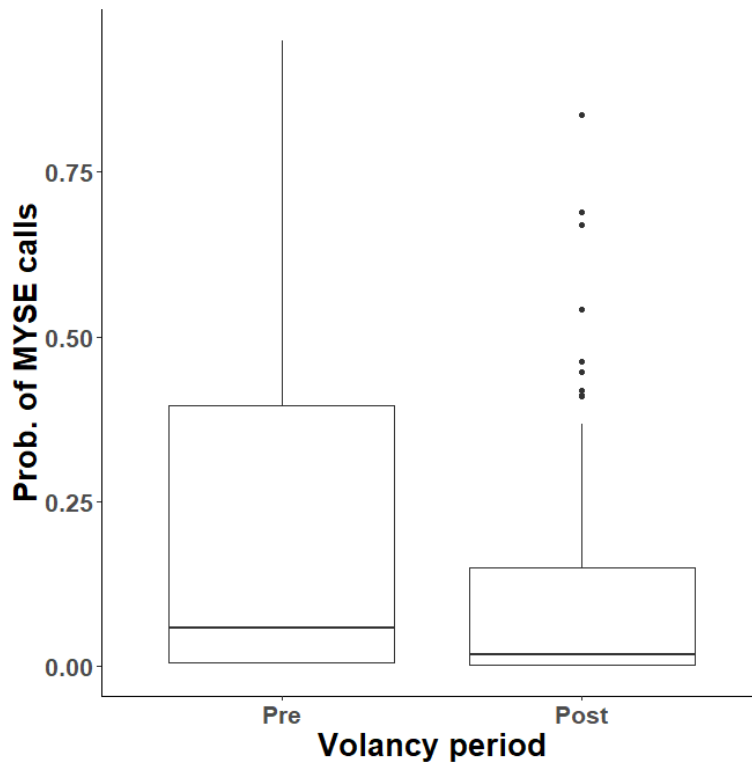


Figure 0-5. Predicted pre- (before June 24) and post- volancy (June 24 and later) probability (Prob.) of activity for northern long-eared bat (*Myotis septentrionalis*; MYSE) acoustic activity (2015–2020). Boxes represent 50% of the data, horizontal line in the box represents the median, whiskers represent the extent of roughly 97% of the data, and dots represent outliers.

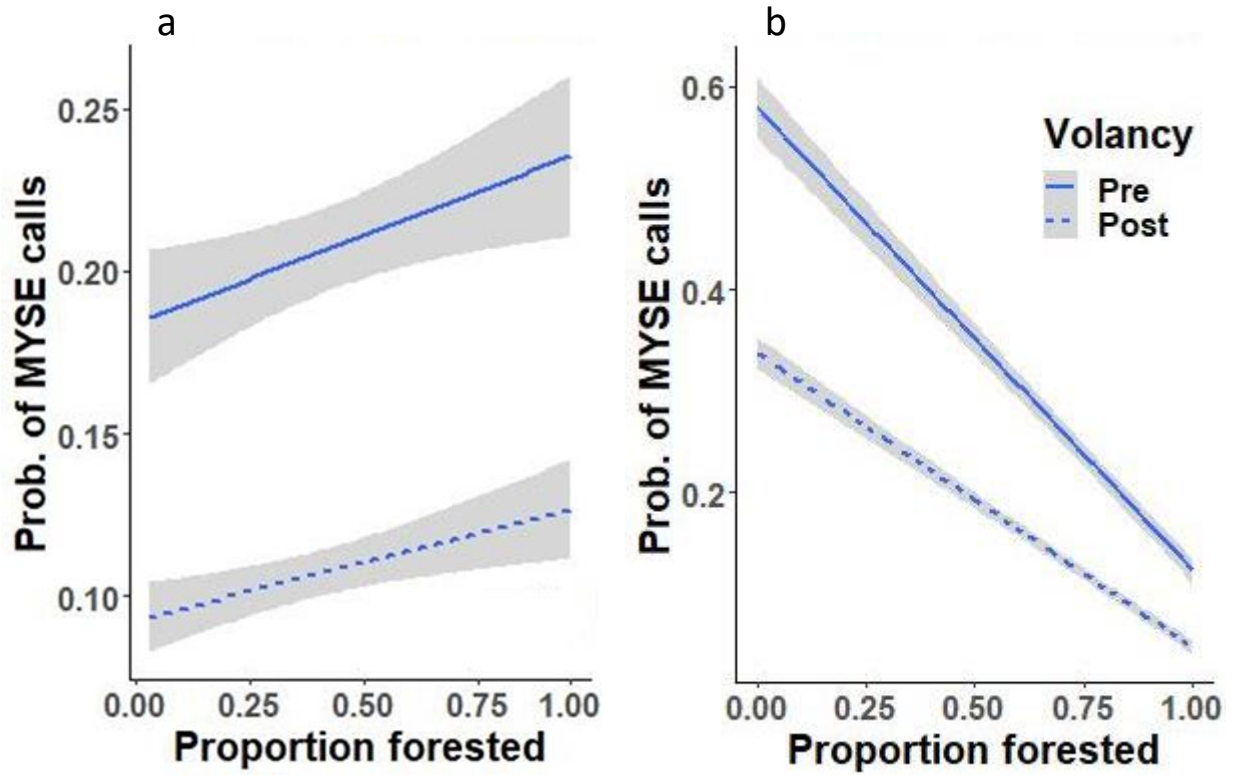


Figure 0-6. Predicted effects of percent forest cover (a) within the presence area polygon and (b) within 30 m of acoustic sites on predicted probability (Prob.) of northern long-eared bat (*Myotis septentrionalis*; MYSE) nightly calls (2015–2020). Note the different y-axis scales. Shaded areas: 95% confidence intervals; solid lines: pre-volancy period (before June 24); dashed lines: post-volancy period (June 24 and later).

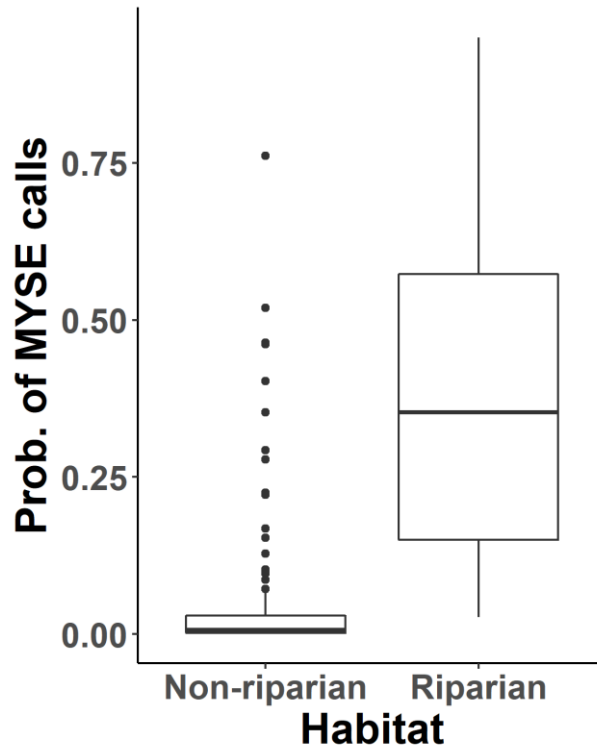


Figure 0-7. Predicted effects of riparian habitat on probability of activity for northern long-eared bats (*Myotis septentrionalis*; MYSE), 2015–2020. Boxes represent 50% of the data, horizontal line in the box represents the median, whiskers represent the extent of roughly 97% of the data, and dots represent outliers.

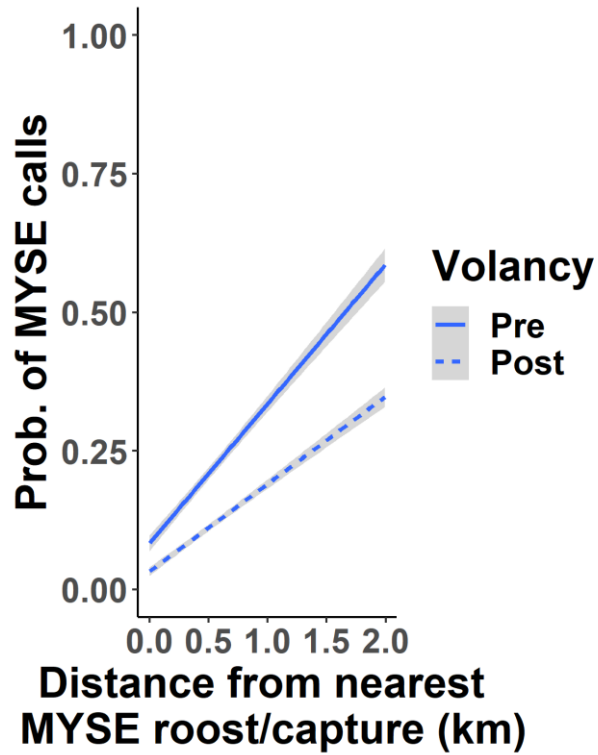


Figure 0-8. Predicted effects of distance from nearest northern long-eared bat (*Myotis septentrionalis*; MYSE) capture site or roost on predicted probability of nightly activity (2015–2020). Shaded areas: 95% confidence intervals; solid lines: pre-volancy period (before June 24); dashed lines: post-volancy period (June 24 and later).

Bat activity patterns relative to temporal and weather effects in a temperate coastal environment

Abstract

The northeastern and mid-Atlantic coasts of the United States are important summer maternity habitat and seasonal migratory corridors for many species of bats. Additionally, the effects of weather on bat activity are relatively unknown beyond coarse nightly scales. Using acoustic detectors, we assessed nightly and hourly activity patterns for eight species of bats over 21 consecutive months at Fire Island National Seashore, New York. The site is an important bat conservation area because it hosts one of the few confirmed northern long-eared bat (*Myotis septentrionalis*) maternity colonies in the region despite their widespread extirpation due to White-nose Syndrome (WNS). There have been no reported captures of little brown bats (*M. lucifugus*), Indiana bats (*M. sodalis*), or tri-colored bats (*Perimyotis subflavus*) at the site post-WNS. Overall, we found mean hourly temperature, time since sunset, day of year, and year to be the most important predictors of bat activity levels for all examined species. Most non-hibernating, migratory species in our study demonstrated a positive relationship to mean temperature at the hourly timescale, whereas cave-hibernating bats tended to show a negative relationship to mean temperature during the time of year when they are expected to be active. Although most bat activity occurred in the late spring through early autumn, peaking in summer, some activity occurred periodically in the winter months, mostly attributable to the big brown bat (*Eptesicus fuscus*) and silver-haired bat (*Lasionycteris noctivagans*) phonic group. Unexpectedly, relationships of bat activity to wind and precipitation were largely equivocal. Initial presence (as early as March 30) and departure (between November 1–4) for northern long-eared bats at our study area occurred earlier in the spring and later in the fall than occurs for inland populations, suggesting that the species overwinters on Long Island rather than at inland karst caves or mines. A peak in spring activity characteristic of migratory behavior in the central Appalachians and Atlantic Coast was not observed at Fire Island, although Eastern red bats (*Lasiurus borealis*) and hoary bats (*L. cinereus*) – both migratory species – did show a notable rise in activity in the late summer and early fall, suggesting these populations may migrate to and from Fire Island. Understanding the temporal and weather relationships to bat activity in this coastal environment may have important implications for tailoring more effective conservation and management strategies by identifying optimal timing for surveys, tracking bats during peak migratory windows, and providing insights that minimizes impacts to extant bats from activities such as wind-energy development or land management, i.e., forestry.

Introduction

In temperate environments, many bat species make seasonal migrations between winter and summer habitats and often are exposed to anthropogenic-induced mortality (i.e., collisions with wind turbines) during these movements (Arnett et al., 2008; Arnett and Baerwald, 2013; Kunz et al., 2007). For example, (Smallwood and Bell, 2020) recently estimated bat fatalities from wind turbine strikes in the United States exceed 1.7 million bats annually, a number that may grow as this energy production sector expands. Additionally, populations of cave-hibernating bats are being reduced by White-nose Syndrome (WNS), which has resulted in population declines of over 90% and local extirpations of many affected species such as the little brown bat (*Myotis lucifugus*), the northern long-eared bat (*M. septentrionalis*), and the tri-colored bat (*Perimyotis subflavus*; Cheng et al., 2021; Frick et al., 2010; Turner et al., 2011). Mortality-causing events such as these may result in changes to species-protection status. For example, the northern long-eared bat was listed as a federally-threatened species under the Endangered Species Act in 2015 (ESA; (Silvis et al., 2016; U.S. Fish and Wildlife Service, 2015a) due to landscape-scale population declines related to WNS, and the little brown bat and tri-colored bat are currently petitioned for listing (U.S. Fish and Wildlife Service, 2022; U.S. Geological Survey, 2022).

In addition to possible changes in regulatory status of impacted species, negative impacts to ecosystem integrity as a result of declining bat populations are a concern. Although WNS is not a human-health threat, bat population declines and/or extinction can have cascading ecological effects that can impact other biodiversity components, forestry and agriculture (Frick et al., 2010; Jachowski et al., 2014; Kunz et al., 2011; Maine and Boyles, 2015).

Maternal colonies of northern long-eared bats have persisted in coastal areas of the Northeast and mid-Atlantic (De La Cruz et al., 2020; Dowling et al., 2017; Dowling and O'Dell, 2018; Grider et al., 2016) likely because these bats inhabit hibernacula free of WNS or spend less time in WNS-infected caves by arriving later in fall and departing earlier in spring, or by remaining partially active throughout winter months. If coastal areas serve as refugia for surviving residual cave bat communities in the post-WNS environment or as important non-hibernating migratory bat flyways, understanding temporal patterns of presence and activity is paramount for guiding management efforts in these important bat conservation areas.

To date, little research has examined bat responses to climatic conditions long-term at the hourly scale or across a full suite of seasons, particularly in the northeastern United States (Grider et al., 2016; Johnson et al., 2011; Nocera et al., 2019a). Documenting hourly patterns of bat activity broadly are needed to inform wind-energy best management practices that help reduce bat mortality (i.e., minimum wind cut in speeds and variation in nightly and seasonal bat activity). However, examining bat activity at the hourly timescale also can help elucidate fine-scale or site-specific external triggers that influence bat activity directly relatable to mitigating wind-energy impact. Jachowski et al. (2014) showed that WNS-impacts to community composition that resulted in changes in niche-partitioning was most apparent when fine-scaled temporal bat activity was examined. Similarly, because nightly temporal patterns may vary by season and weather, there is a need for these patterns to be assessed over an annual timeframe.

Bat activity has a positive relationship with temperature (Cryan and Brown, 2007; Ruczyński and Bartoń, 2020; Whitaker and Rissler, 1992). Additionally, bat activity typically declines with increasing precipitation and wind speed as well as changes in barometric pressure (Dechmann et al., 2017; Muthersbaugh et al., 2019a; Patriquin et al., 2016; Smith and McWilliams, 2016). Weather affects not only bat activity and prey availability, but also plays a role in the timing and pattern of longer-distance migratory movements, i.e., to hibernacula or overwintering grounds in the case of non-hibernating bats (Muthersbaugh et al., 2019a, 2019b).

Relationships between weather conditions and activity among bat species have the potential to be more pronounced in coastal areas, which tend to be windier, with less extreme temperature ranges compared with inland areas along the Atlantic Coast (Grider et al., 2016). For this study, we investigated the influence of weather conditions (i.e., temperature, wind speed, and precipitation) on hourly bat activity of bats in a northeastern coastal environment throughout the year at the William Floyd Estate (WIFL) portion of Fire Island National Seashore, NY, USA. This land remains as a relatively intact forest block along the eastern periphery of the New York City metro area, and because of its location along the Atlantic Coastal Plain, WIFL is believed to provide critical foraging and roosting habitats for migratory and cave-hibernating bats species in the region. Accordingly, our objectives were to use acoustic sampling methods to determine hourly activity patterns for eight species of bats at WIFL and compare the levels of activity to local weather data over the course of the active season. Additionally, we investigated whether or not ecologically similar bats, such as *Myotis* species and tri-colored bats (cave-hibernating species), local year-round resident big brown bats (*Eptesicus fuscus*), and non-hibernating migratory tree bats such as silver-haired bats (*Lasionycteris noctivagans*), eastern red bats (*Lasiurus borealis*), and hoary bats (*L. cinereus*) would exhibit similar responses to weather variables (Ford et al., 2011; Nocera et al., 2019a). In addition to informing wind-energy development, understanding these patterns may give

managers insights into the timing of potential land management stewardship actions, therefore minimizing any negative impacts to bats when they are most vulnerable (early hibernation emergence and during the maternity season before young are volant). Moreover, determining these patterns in warmer, more moderate coastal areas may provide insights into the responses of bats and/or their plasticity in response to future climate changes and these inferences would perhaps be applicable to bats in inland areas (Gorman et al., 2022).

Materials and methods

Study area

We conducted our study at the 248-ha WIFL unit of Fire Island National Seashore (40.77°N, 72.82°W) in Suffolk County, New York, USA (Figure 0-1). Located on the Atlantic Coastal Plain, the regional climate was classified as humid temperate with a maritime influence, and averaged 180–200 frost-free days per year. Precipitation was evenly distributed throughout the year, with a mean of 119.71 cm (U.S. Climate Data, 2020), though the coast often could be subject to heavy precipitation events from tropical depressions and winter nor'easter storms (NOAA's National Centers for Environmental Information, 1996). The vegetation cover consisted of mature coastal oak (*Quercus* spp.)-ericaceous heath forest (65%), tidal marshes and wetlands (25%), and open fields (5%). The remainder of the estate was developed land (Klopfer et al., 2002). The entire property sat at an elevation <2 m above sea level. Common tree species at WIFL were pitch pine (*Pinus pungens*), red maple (*Acer rubrum*), black locust (*Robinia pseudoacacia*), white oak (*Q. alba*), scarlet oak (*Q. coccinea*), and sassafras (*Sassafras albidum*). The understory was dominated by dense greenbrier (*Smilax* spp.) and poison ivy (*Toxicodendron radicans*; Klopfer et al., 2002).

Acoustic monitoring

In April of 2018, we deployed nine stationary SM4BAT zero-crossing/frequency division acoustic detectors with SMM-UI omnidirectional microphones (Wildlife Acoustics, Maynard, MA, USA) within WIFL along single-track roads, trails, and fields in forest and marsh-edge habitats. Of these, we removed four at the end of July in 2018 for other research deployments and maintained the five recorders through the following year. In April of 2019, we deployed an additional six detectors ($n = 11$) on previously unmonitored trails near northern long-eared bat maternity roosts that we identified in 2018

during mist-net surveys (Table 0-1, Figure 0-1). Microphones were mounted two meters off the ground on telescoping poles along road/trail corridors or open fields to maximize echolocation call quality acquisition (De La Cruz et al., 2020; Nocera et al., 2019a). We set detectors to record from 30 min prior to sunset until 30 min following sunrise.

We used Kaleidoscope Pro (Wildlife Acoustics, Maynard, MA, USA; Version 5.1.0; Classifier Version 5.1.0; 0 Sensitivity Setting²) to process echolocation calls following U.S. Fish and Wildlife Service acoustic monitoring protocols (U.S. Fish and Wildlife Service, 2015b). We set a minimum threshold of three pulses per call file to minimize bat species misclassification (Muthersbaugh et al., 2019a). Following species lists of known or suspected bats for the Long Island area (Seatuck Environmental Association, 2017), we included the following species as potentially occurring at WIFL: big brown bats, silver-haired bats, Eastern red bats, hoary bats, little brown bats, Indiana bats, northern long-eared bats, and tri-colored bats. We further visually examined a random sample of calls classified with high confidence per species per detector per night according to protocols set forth by the North American Bat Monitoring Program ($n = 36,232$; Reichert et al., 2018) to determine accuracy of species identification and presence, but did not change calls from software classifications to avoid introducing additional bias (Nocera et al., 2019b). Because of previously documented misclassification between little brown and Indiana bats and big brown and silver-haired bats (U.S. Geological Survey, 2019), we combined these species into two phonic groups for analysis, respectively (Austin et al., 2018; Johnson et al., 2008; Menzel et al., 2002). We concluded that the classifications provided by the software were acceptable to continue with our analysis (Nocera et al., 2019b), recognizing that some inherent error remained.

To assess the effects of weather on bat activity, we obtained hourly weather variables from Aviation Routine Weather Reports (Iowa State University, 2022) that were measured by Automated Surface Observing Systems (ASOS) at the nearby Shirley/Brookhaven Airport seven kilometers north of WIFL. These variables included the mean hourly wind speed (KPH), mean hourly temperature (°C), and total hourly precipitation (mm) for each night of our study.

Statistical analyses

We used R version 3.6.1 to perform all statistical tests and analyses for assessing bat activity with weather and temporal periods (R Core Team, 2020). We tested for multicollinearity among our predictor variables using the *corrplot* package (Wei and Simko, 2021) and we found no correlation $\geq |0.6|$ between

² Overall correct classification accuracy for each species in this assembly state is as follows: big brown bat (77%), Eastern red bat (71%), hoary bat (13%), silver-haired bat (41%), little brown bat (69%), northern long-eared bat (81%), Indiana bat (64%), tri-colored bat (64%; U.S. Geological Survey, 2019).

predictors, and therefore none were removed from further analyses. We combined echolocation call totals into hourly blocks per night for each acoustic detector and assigned values of zero to detectors when no calls were recorded for a given hour. We calculated time since sunset of any given hour using the *suncalc* package (Thieurmel and Elmarhraoui, 2020).

To visualize seasonal trends of bat activity at WIFL, we modeled nightly bat activity by species using generalized additive models (GAMs) using *ggplot2* (Wickham, 2016). To remove biases of non-detections during the winter, we selected an “active” window by using just the first Day of year of acoustic detection to last Day of year of acoustic detection for each bat species or phonic group (Table 0-2). Because knowing the timing of bat arrival and departure as well as summer peaks (i.e., parturition and juvenile volancy) are important to inform site-level conservation measures to protect bats, we then fit GAM trend lines post hoc for every bat species/phonic group using the *ggplot2* package for better visualization of these activity patterns (Figure 0-2; Wickham, 2016). We calculated a peak activity window start date when the lower confidence level of the GAM >0 in the spring and ≥ 0 in the fall (Table 0-2, Figure 0-2). Prior to analysis, we transformed Day of year to radians using the package *aspace* (Bui et al., 2012) to make it a circular variable (i.e., the last day of the year [365] is followed by the first day of the year [1]).

For estimating hourly bat activity by species, we created a set of 36 candidate models relative to wind, temperature, precipitation, time since sunset, Day of year, and year (2018 or 2019). We included interaction terms between all of the variables using generalized linear mixed models (GLMMs) with a zero-inflated negative binomial distribution function to account for the non-normality of our echolocation count data and excess zeros (attributed to minimal activity). We set our detector (‘site’) covariate as a random variable using the *glmmTMB* package (Brooks et al., 2017). Hour was the smallest unit of time, enabling us to avoid the misleading effect of partial night rain on bat activity. We scaled all weather variables to 0–1 prior to analyses using the R package *BBmisc* (Bischof et al., 2017) so that the effect size for beta (β) coefficients could be easily compared across variables. Following GLMM model selection, we then ranked models using Akaike’s information criteria (AIC; Burnham and Anderson, 2002). For each analysis, we only considered the top-ranking model to be the best-supported model if no other competing model was within two Δ AIC units for any bat species (Burnham and Anderson, 2002). Model R^2 values were calculated using the *performance* package (Lüdtke et al., 2021).

Results

From April 2018 to December 2019, we recorded acoustic data for 63 384 h and 4530-detector nights over 595 calendar days at WIFL (Table 0-1). We detected all target species for our study with the big brown/silver-haired phonic group, Eastern red bats, and hoary bats being most frequently detected (proportion of recording nights with a positive species/species group detection for each detector; Table 0-3). Recording was not continuous at all detectors throughout this period due to periodic malfunctions, i.e., battery depletion, and because some detectors were only present during the maternity season. Peak activity windows as calculated using GAM trend lines ranged from mid-February/late March to September for all species except northern long-eared bats that had a peak ending in late July Table 0-2.

Eastern red bats, northern long-eared bats, and hoary bats had two distinct waves of activity throughout the summer (Figure 0-2). There were no competing GLMM models (within two Δ AIC units) within species and species groups, therefore, we selected the top model for each according to AIC rank (Table 0-4). Model fit was low for all models ($R^2 \leq 0.14$), suggesting a large portion of variability in activity was not captured by our selected weather variables. Though predictor interactions and presence in the models varied somewhat by species for the top models, mean hourly temperature, Day of year, and year were significant predictors of hourly activity for all species, except for year, which was not significant for Eastern red bats (Table 0-5 & Table 0-6). Mean hourly wind speed and total hourly precipitation were not significant predictors in the top model for any species examined. We excluded tri-colored bat from GLMM analysis because of low detection rates.

For each species and species group, mean hourly temperature was a significant predictor of hourly bat activity, whereas mean hourly wind speed and total hourly precipitation were not included (Table 0-6). Hourly activity had a positive relationship with mean temperature for the big brown bat/silver-haired bat phonic group, Eastern red bats, and hoary bats and a negative relationship for the little brown bat/Indiana bat phonic group and northern long-eared bats (Table 0-6).

The big brown bat/silver-haired bat phonic group activity had a negative relationship to time since sunset, meaning their activity predominated at the beginning of the night. Eastern red bat activity had a positive, albeit weak, relationship to time since sunset, as their activity was more evenly spaced throughout the night. Northern long-eared bat activity had a stronger positive relationship to time since sunset (meaning, as time since sunset increased, so did acoustic activity levels), indicating later foraging bouts in the evening and/or closer to sunrise.

Hoary bats showed a very strong positive relationship to year and Day of year. However, this relationship was reversed when examined in the context of the year*Day of year interaction (the relationships became negative). When examined in the context of the interaction between all three

variables (year, Day of year, and temperature) this relationship was positive. The little brown bat/Indiana bat phonic group demonstrated a negative relationship to individual temporal predictors.

Discussion

Most bat activity at WIFL is predicted to occur between 10 and 30°C regardless of the strength or direction of the modeled relationship. The midpoint at which activity decreases slightly appears to be around 20°C, particularly for Eastern red bats (Figure 0-3). Nonetheless, *Myotis* species were more active at lower temperatures at the hourly timescale. We attributed this to either being a result of an early spring arrival and initial summer residency in or near WIFL, rather than migratory species that would pass through later in the summer when temperatures are higher and/or after these cave bats have already dispersed.

As the only meteorological variable included in our top models, temperature likely plays a role in triggering either movement along migratory routes (Muthersbaugh et al., 2019a) or establishment of summer residency of cave-hibernating bats (Faure-Lacroix et al., 2020; Humphrey, 1975; Tuttle and Stevenson, 1982); this could be a result of higher prey availability in warm weather (Turbill, 2008). The seasonal trends in activity among all species show an initial rise in activity approximately between 29 May and 19 July (days 150–200), which was likely due to an increase in foraging by pregnant and lactating females (Deeley, 2019). This was followed by a decline and subsequent, smaller rise in activity at the end of the summer season (Figure 0-2). Depending on species, this fluctuation could be a migration pulse or an indication of newly volant pups appearing on the landscape (Ford et al., 2011; Nocera et al., 2019a).

(Cryan et al., 2014; Lacki, 1984) suggested that females and males of the same bat species may react to different environmental cues, although the positive association with temperature still holds regardless of sex (Baerwald and Barclay, 2011). It is likely that many of our call files that were attributed to *Myotis* species early in the year are foraging females from resident maternity colonies, as opposed to the migratory bats which could be either sex. This assumption is further bolstered by our mist-net captures at WIFL in 2018 and 2019, whereby only two out of 22 captured northern long-eared bats were adult males.

In the context of the mean hourly temperature*year interactive term, the little brown bat/Indiana bat phonic group was more likely to be active in warmer temperatures despite declines in overall acoustic

activity from the first year to the second (the decline presumably due to continued WNS impacts or simply normal annual variability). The decline in activity at higher temperatures may have been a sampling artifact of our “active” season window used in the analysis (1 January–29 December). The relationship between activity and temperature looks negative when plotted against one another, however there are more hours with >0 calls at higher temperatures and a peak predicted around 10°C (Figure 0-3). This could indicate residency early in the year and dispersal by late summer when temperatures could be more consistently higher than 10°C. Francl et al. (2012) noted a narrowing in reproductive windows for northern long-eared bats and little brown bats post-WNS. Considering the Day of year or year interaction with temperature, it is likely that WIFL does not support active maternity colonies in close proximity. Therefore, for our data, the little brown/Indiana bat activity relationship with temperature is relative to season; foraging during temperatures that are high for April nights (10°C) but that would not be considered high in August. These species’ presence early in the spring and later in the fall reduced the direct strength of the relationship between activity and temperature when all other values were held constant (Table 0-6, Figure 0-2).

In general, at WIFL, northern long-eared bats and Eastern red bats are more active later in the night, with hourly activity occurring earlier in the night as the year progresses (Table 0-6). This pattern indicates these species forage earlier in the night as decreasing nighttime temperatures likely cause insects to be more active earlier in the night. Alternatively, the big brown bat/silver-haired bat phonic group was more acoustically active closer to sunset, suggesting they forage primarily closer to sunset or are emerging from roosts within the park close to sunset and foraging elsewhere until returning to roost in the park again close to sunrise. As the year progressed that pattern shifted, suggesting that as the summer proceeds, these bats may exhibit longer or more numerous foraging bouts later in the night.

Hoary bats were the only species analyzed where Day of year alone was a positive predictor of activity, indicating that WIFL area was used as a late summer-fall southward migration corridor but less so in the spring during northward migration. Whether this was a function of a northward migration more diffuse in space and time (Cryan, 2003), or use of a non-coastal route is unknown. It is possible these positive relationships were sampling artifacts, i.e., more detectors deployed in the fall of the second year. Unfortunately, our initial April start date in 2018 may have missed the initial hoary bat pulse that year if migration occurred prior to that date, therefore masking our ability to document a strong spring migration signal.

A long-term study to confirm the viability of the bat communities at WIFL using in-hand confirmations of all species being recorded and their reproductive condition, as well as recording subtle

corresponding meteorological changes across several years, could further elucidate these patterns across species. Increased researcher participation in large-scale, long-range monitoring projects such as the Motus Wildlife Tracking System (Motus.org) would allow us to pinpoint migratory windows for certain species, and late-season radio-tagging of cave bats would provide opportunities for identifying local hibernation sites.

Consistently rising temperatures due to climate change could shorten the hibernation windows for cave bats and allow for greater relative body mass either by increased prey abundance or smaller energetic costs, making them less susceptible to WNS-mediated mortality (Faure-Lacroix et al., 2020; Grider et al., 2016; Haarsma et al., 2019; Loeb and Winters, 2013; Warnecke et al., 2012). Entering torpor for shorter duration, with higher fitness, or in local, aberrant hibernacula (such as anthropogenic structures or trees), may decrease the temporal exposure to fungal loads. In our own research on Long Island at WIFL – as well as that of Dowling and O’Dell (2018) in Massachusetts – remaining northern long-eared bats along the northeastern coast are showing little physical evidence of WNS, despite occasionally testing positive for *Pseudogymnoascus destructans* spores (the causative agent of WNS). Nonetheless, in a coastal environment lacking typical hibernacula such as caves and mines, temperatures in available “aberrant” hibernacula may be less stable (Zahn, 1999); this may lead to a higher likelihood of mortality via exposure to freezing temperatures (Brack, 2007; Humphrey, 1975; Tuttle and Stevenson, 1982), or frequent arousals from torpor encouraged unseasonably warm temperatures, depleting fat reserves during a time when successful foraging is unlikely (Cryan et al., 2010; Perry and Jordan, 2020; Ruczyński et al., 2005; Speakman and Rowland, 1999).

Ongoing climate change has already affected evolutionary shifts in the distribution of plant species (Fitter and Fitter, 2002; Franks et al., 2007; Perry, 2018) as well as range expansions and changes in migration and reproductive timing for insects and birds (Chen et al., 2011; Hitch and Leberg, 2007; Parmesan and Yohe, 2003; Thomas, 2010, p. 2; Zuckerman et al., 2009), raising expectations for ecological shifts among other communities (Faure-Lacroix et al., 2020; Perry, 2018). With climate change, the migratory distances from maternity areas to overwinter areas may decrease for areas such as WIFL that are expected to shift to the transition between temperate and warm-temperate environments (Odom and Ford, 2020). Future climates may allow tree bats to remain in the region with shorter and more moderate winters, or at a minimum allow for a delay in the costly energetic and physiological demands of migration if there are consistent food supplies locally (Cryan, 2003; Cryan et al., 2014; Grider et al., 2016). If they forego migration altogether and range extents are modified (Andersen et al., 2017; Humphries et al., 2002; Jones et al., 2009; Perry, 2018), this could have cascading effects on reproductive timing, their ecosystem service role (Boyles et al., 2011; Maas et al., 2013; Rydell et al., 2010), or as

bioindicators (Bender and Hartman, 2015; Jones et al., 2009). It could also increase the chance that these bat species are caught in unseasonable, severe cold snaps that may still occur in future warmer climates at these higher latitudes (Newton, 2007). Regardless, because some elements of climate change in terms of warmer temperatures and changes in potential vegetation are predicted to occur more rapidly along the coast, near-term responses of bats at Northeast USA sites such as WIFL may provide insights for longer term changes in inland, continental regions (Chen et al., 2011; Zuckerberg et al., 2009).

Although temperature can fluctuate between years, variability in temperature (especially extremes) is predicted to occur more frequently and be greater due to climate change processes (Bell et al., 2004; Viceto et al., 2019). Our research at WIFL may suggest a need to foster more discussion about management guidelines designed to minimize impact to bats, especially when considering land management restrictions that are date-based such as the 4(d) Rule for northern long-eared bats (U.S. Fish and Wildlife Service, 2015a). The 4(d) Rule provides guidelines for allowable activities that might impact a threatened species in order to maximize protections during sensitive life stages and minimize requirements for those implementing the conservation actions, i.e., avoiding a “take” designation that would otherwise occur under an Endangered listing. However, our observations from WIFL may indicate that in coastal areas, and perhaps in the future for inland areas as climate change proceeds, shifts in activities such as timber harvesting, prescribed burning or development and current curtailment windows (which are designed to protect maternity activity and non-volant juveniles from harm) may need to be considered. The peak activity window calculated with the GAM trend lines suggests that we may need to monitor for species of concern earlier in the year than we initially thought. Similarly, for migratory tree bats, less seasonally-predictable temperatures, i.e., higher early spring temperatures or later fall temperatures in the future, could make anticipating migratory pulses more difficult and thus complicate seasonal-based efforts to match wind-energy mortality mitigation standards with dates.

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Tables

Table 0-1. Deployment window, total recording nights, and total recording hours for each detector at the William Floyd Estate, Fire Island National Seashore, New York, Apr 2018–Dec 2019 (see Figure 0-1 for detector locations).

Detector ID	Deployment window	Total recording nights	Total recording hours
01	25 Apr 2018–24 Jul 2018	93	1127
02	26 Apr 2018–30 Nov 2019	582	8305
03	25 Apr 2018–24 Jul 2018	93	1129
04	25 Apr 2018–26 Jul 2018	95	1149
05	25 Apr 2018–4 Dec 2019	576	8339
06	25 April 2018–8 Dec 2019	595	8609
07	25 Apr 2018–20 Jun 2018	59	717
08	25 Apr 2018–8 Dec 2019	595	8604
09	25 Apr 2018–9 Dec 2019	595	8599
10	20 Jun 2018–2 Dec 2019	515	7506
11	16 Mar 2019–1 Aug 2019	141	1786
12	16 Mar 2019–1 Aug 2019	141	1786
13	16 Mar 2019–22 Jul 2019	30	326
14	16 Mar 2019–1 Aug 2019	140	1774
15	16 Mar 2019–1 Aug 2019	140	1774
16	16 Mar 2019–1 Aug 2019	140	1774
Total		4530	63 384

Table 0-2. Active window beginning and end dates for each species used in the analyses. Dates were chosen as first and last acoustic detections, respectively, for each species across both years. Peak activity window calculated using confidence intervals on generalized additive model trend lines for each species. Numbers outside parentheses are Day of year numbers as used in analyses.

Species/phonic group	First day of detection	Peak activity	Last day of detection
Big brown bat/silver-haired bat	1 (1 Jan)	48–267 (17 Feb–24 Sep)	363 (29 Dec)
Eastern red bat	74 (15 Mar)	70–268 (11 Mar–25 Sep)	349 (15 Dec)
Hoary bat	1 (1 Jan)	84–255 (25 Mar–12 Sep)	362 (28 Dec)
Little brown bat/Indiana bat	74 (15 Mar)	60–270 (1 Mar–27 Sep)	356 (22 Dec)
Northern long-eared bat	89 (30 Mar)	50–201 (19 Feb–20 Jul)	308 (4 Nov)

Table 0-3. Proportion of nights in which a species or species group was acoustically present at each detector. Detectors marked with * were deployed for the duration of the study, including winter months (see Table 0-1 for exact deployment dates). Big brown bats (*Eptesicus fuscus*) and silver-haired (*Lasionycteris noctivagans*) bats were combined into one phonic group for this analysis, as were little brown bats (*Myotis lucifugus*) and Indiana bats (*M. sodalis*).

Detector ID	Big brown/silver-haired bat	Eastern red bat	Hoary bat	Little brown/Indiana bat	Northern long-eared bat	Tri-colored bat
01	0.75	0.46	0.60	0.20	0.06	0.00
02*	0.39	0.26	0.30	0.23	0.08	0.04
03	0.70	0.57	0.55	0.69	0.69	0.19
04	0.34	0.14	0.20	0.12	0.39	0.00
05*	0.60	0.39	0.38	0.45	0.28	0.16
06*	0.47	0.40	0.31	0.29	0.11	0.08
07	0.63	0.07	0.27	0.20	0.14	0.00
08*	0.49	0.28	0.20	0.32	0.11	0.04
09	0.10	0.11	0.08	0.05	0.01	0.01
10*	0.50	0.35	0.24	0.45	0.38	0.08
11	0.31	0.07	0.21	0.10	0.06	0.01
12	0.34	0.21	0.36	0.20	0.05	0.01
13	0.20	0.00	0.00	0.03	0.00	0.00
14	0.67	0.53	0.44	0.17	0.01	0.01
15	0.63	0.54	0.46	0.16	0.18	0.00
16	0.50	0.31	0.32	0.41	0.23	0.13

Table 0-4. Top three competing generalized linear mixed models, associated number of parameters (K), Akaike's information criterion values (AIC), model rankings (Δ AIC), and Akaike weights (ω_i) for predicting species activity during the maternity season at the William Floyd Estate, Fire Island National Seashore, New York (2018 and 2019). Models are written out under the species/group name, and an * denotes an interaction. Temp is mean hourly temperature ($^{\circ}$ C), wind is mean hourly wind speed (KPH), precip is total hourly precipitation (mm), day is Day of year, and hour is time (in hours) since sunset that a particular call sequence occurred. Site is detector site and was included as a random variable. Big brown bats (*Eptesicus fuscus*) and silver-haired bats (*Lasionycteris noctivagans*) were combined into one phonic group; likewise, little brown bats (*Myotis lucifugus*) and Indiana bats (*M. sodalis*) were combined into one phonic group.

Big brown bat/silver-haired bat phonic group	K	AIC	ΔAIC	ω_i	R²
Temp + Day * Year * Hour + Site (random)	12	56 475.79	0.00	1.00	0.13
Temp + Day + Year + Hour + Site (random)	8	56 587.87	112.08	4.59e-25	0.14
Wind + Precip + Year * Day * Hour + Site (random)	13	56 807.40	331.61	9.81e-73	0.07
Eastern red bat					
Temp + Day * Year * Hour + Site (random)	12	39 091.74	0.00	1.00	0.08
Temp * Day * Year + Site (random)	11	39 095.53	0.15	0.13	0.06
Temp + Day + Year + Hour + Site (random)	8	39 129.78	38.04	4.77e-09	0.07
Hoary bat					
Temp * Day * Year + Site (random)	11	24 604.16	0.00	1.00	0.05
Temp + Day * Year * Hour + Site (random)	12	24 757.33	153.17	5.48e-34	0.08
Temp + Day * Year + Site (random)	8	24 808.39	204.23	4.48e-45	0.08
Little brown bat/Indiana bat phonic group					
Temp * Day * Year + Site (random)	11	25 980.05	0.00	1.00	0.06
Wind + Precip + Year * Day * Hour + Site (random)	13	26 005.15	25.10	3.55e-06	0.07
Temp + Day * Year * Hour + Site (random)	12	26 012.90	32.85	7.36e-08	0.07
Northern long-eared bat					
Temp + Day * Year * Hour + Site (random)	12	12 757.44	0.00	0.86	0.11
Wind + Precip + Year * Day * Hour + Site (random)	13	12 761.11	3.67	0.14	0.14
Day * Year * Hour + Site (random)	11	12 773.53	16.09	2.76e-04	0.13

Table 0-5. All candidate models tested in analyses; null model also tested but not included in table. An * denotes an interaction. Temp is mean hourly temperature (°C), wind is mean hourly wind speed (KPH), precip is total hourly precipitation (mm), day is Day of year, and hour is time (in hours) since sunset that a particular call sequence occurred. Site is detector site and was included as a random variable.

Model
Day + Site (random)
Day + Year + Site (random)
Temp + Site (random)
Wind + Day + Year + Site (random)
Precip + Day + Year + Site (random)
Temp + Wind + Site (random)
Temp * Wind + Site (random)
Temp + Precip + Site (random)
Temp * Precip + Site (random)
Wind + Precip + Site (random)
Wind * Precip + Site (random)
Temp + Wind + Precip + Site (random)
Day * Year + Site (random)
Wind + Year + Site (random)
Wind + Precip + Year + Site (random)
Wind * Precip + Year + Site (random)
Wind + Precip + Day + Year + Site (random)
Wind + Precip + Day * Year + Site (random)
Precip + Year + Site (random)
Wind * Year + Site (random)
Temp + Day + Year + Site (random)
Temp + Day * Year + Site (random)
Temp * Day * Year + Site (random)
Wind + Site (random)
Precip + Site (random)
Day + Hour + Site (random)
Day + Year + Hour + Site (random)
Day * Year * Hour + Site (random)
Wind + Precip + Year + Day + Hour + Site (random)
Wind + Precip + Year * Day * Hour + Site (random)
Wind + Day + Year + Hour + Site (random)
Precip + Day + Year + Hour + Site (random)
Temp + Day + Year + Hour + Site (random)
Temp + Day * Year * Hour + Site (random)
Temp + Wind + Precip + Day + Year + Hour + Site (random)

Table 0-6. Model outputs for top generalized linear mixed model for each species. Coefficient values (β), standard errors (SE), lower 95% confidence limits (LCL), and upper 95% confidence limits (UCL) for best supported generalized linear mixed models predicting species hourly activity during the maternity season at the William Floyd Estate, Fire Island National Seashore, New York (2018 and 2019). Models are written out under the species/group name, and an * denotes an interaction. “Mean hourly temp” is mean hourly temperature, and “Time since sunset” is time (in hours) since sunset that a particular call sequence occurred. Big brown bats (*Eptesicus fuscus*) and silver-haired bats (*Lasionycteris noctivagans*) were combined into one phonic group; likewise, little brown bats (*Myotis lucifugus*) and Indiana bats (*M. sodalis*) were combined into one phonic group.

Predictor	β	SE	LCL	UCL
Big brown bat/silver-haired bat phonic group				
Calls ~ Mean hourly temp + Day of year * Year * Time since sunset + Detector (random variable)				
(Intercept)	1.79	0.34	1.12	2.45
Mean hourly temp	0.08	0.004	0.08	0.09
Day of year	-0.62	0.05	-0.71	-0.53
Year	0.99	0.24	0.52	1.47
Time since sunset	-0.42	0.04	-0.49	-0.35
Day of year * Year	-0.31	0.07	-0.45	-0.18
Day of year * Time since sunset	0.07	0.01	0.05	0.09
Year * Time since sunset	0.10	0.05	0.001	0.20
Day of year * Year * Time since sunset	-0.03	0.01	-0.05	0.003
Eastern red bat				
Calls ~ Mean hourly temp + Day of year * Year * Time since sunset + Detector (random variable)				
(Intercept)	-0.61	0.53	-1.65	0.44
Mean hourly temp	0.08	0.01	0.07	0.09
Day of year	-0.26	0.06	-0.37	-0.15
Year	0.05	0.33	-0.60	0.71
Time since sunset	0.18	0.04	0.11	0.25
Day of year * Year	-0.27	0.10	-0.47	-0.07
Day of year * Time since sunset	-0.06	0.01	-0.08	-0.04
Year * Time since sunset	-0.14	0.06	-0.26	-0.02
Day of year * Year * Time since sunset	0.04	0.02	0.004	0.08
Hoary bat				
Calls ~ Mean temp * Day of year * Year + Detector (random variable)				
(Intercept)	-20.06	1.36	-22.73	-17.39
Mean hourly temp	31.33	2.14	27.14	35.53
Day of year	4.13	0.35	3.45	4.80
Year	19.59	1.40	16.86	22.33
Mean hourly temp * Day of year	-6.95	0.57	-8.07	-5.83
Mean hourly temp * Year	-30.19	2.26	-34.62	-25.75
Day of Year * Year	-5.01	0.38	-5.76	-4.26
Mean hourly temp * Day of year * Year	7.56	0.63	6.33	8.80
Little brown bat/Indiana bat phonic group				
Calls ~ Mean hourly temp * Day of year * Year + Detector (random variable)				
(Intercept)	3.58	0.86	1.90	5.26
Mean hourly temp	-6.75	1.32	-9.34	-4.16
Day of year	-1.20	0.20	-1.58	-0.81
Year	-6.29	1.12	-8.49	-4.09
Mean hourly temp * Day of year	1.71	0.34	1.03	2.38
Mean hourly temp * Year	10.85	1.89	7.14	14.55
Day of year * Year	1.28	0.31	0.67	1.88
Mean hourly temp * Day of year * Year	-2.44	0.52	-3.47	-1.42
Northern long-eared bat				
Calls ~ Mean hourly temp + Day of year * Year * Time since sunset + Detector (random variable)				
(Intercept)	-0.85	0.62	-2.06	0.37
Mean hourly temp	-0.04	0.01	-0.06	-0.02
Day of year	-0.56	0.13	-0.81	-0.30
Year	2.97	0.56	1.88	4.06
Time since sunset	0.37	0.09	0.20	0.53
Day of year * Year	-0.71	0.17	-1.05	-0.37
Day of year * Time since sunset	-0.12	0.03	-0.17	-0.07
Year * Time since sunset	0.05	0.11	-0.17	0.27
Day of year * Year * Time since sunset	0.0003	0.04	-0.07	0.07

Figures

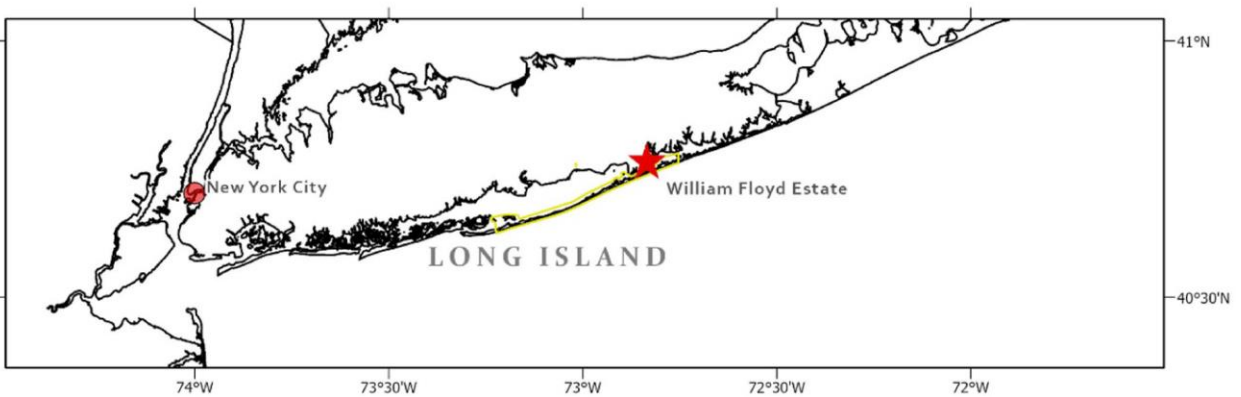
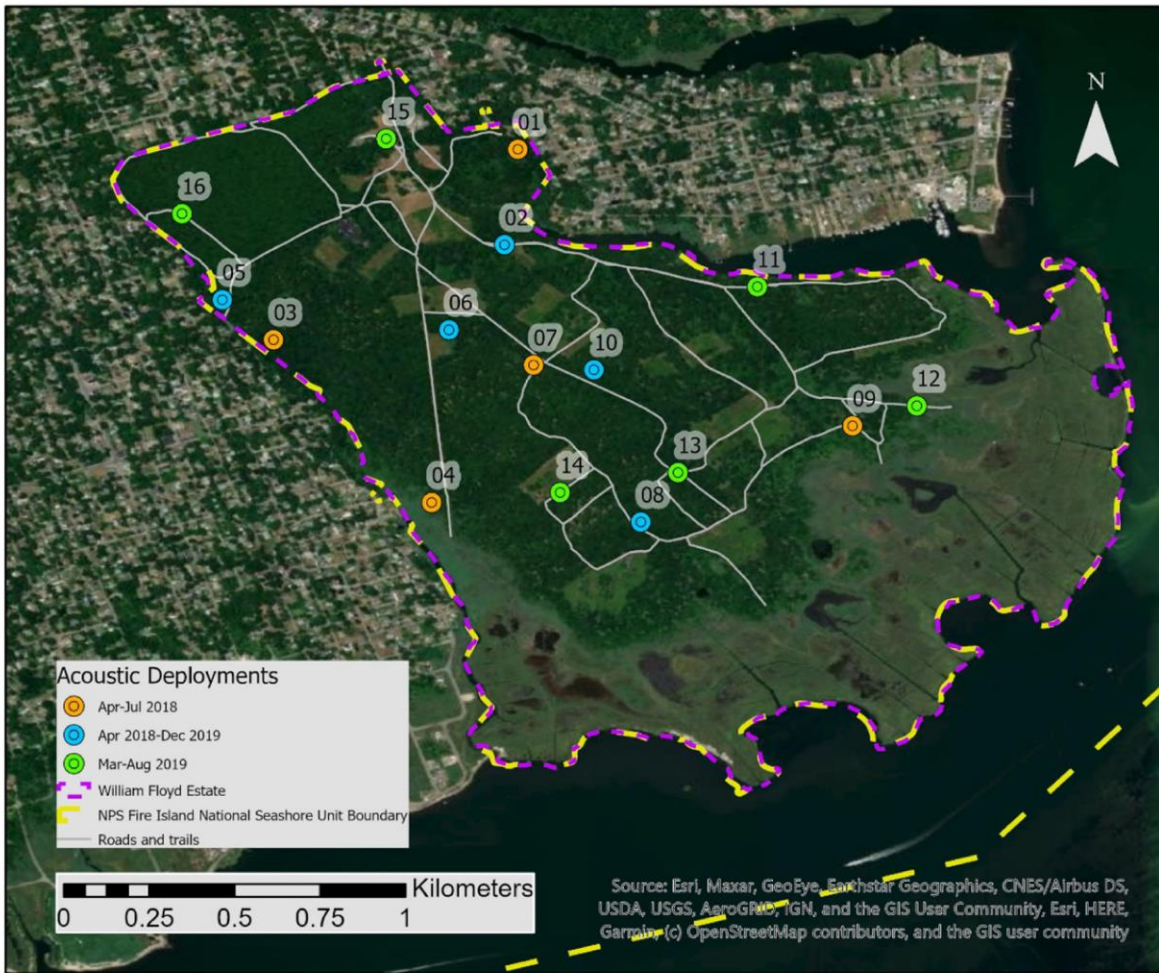


Figure 0-1. Location of acoustic detectors at William Floyd Estate (WIFL; purple dashed line), Fire Island National Seashore (yellow dashed line), New York, USA (Apr 2018–Dec 2019). Gray lines indicate roads and trails throughout WIFL.

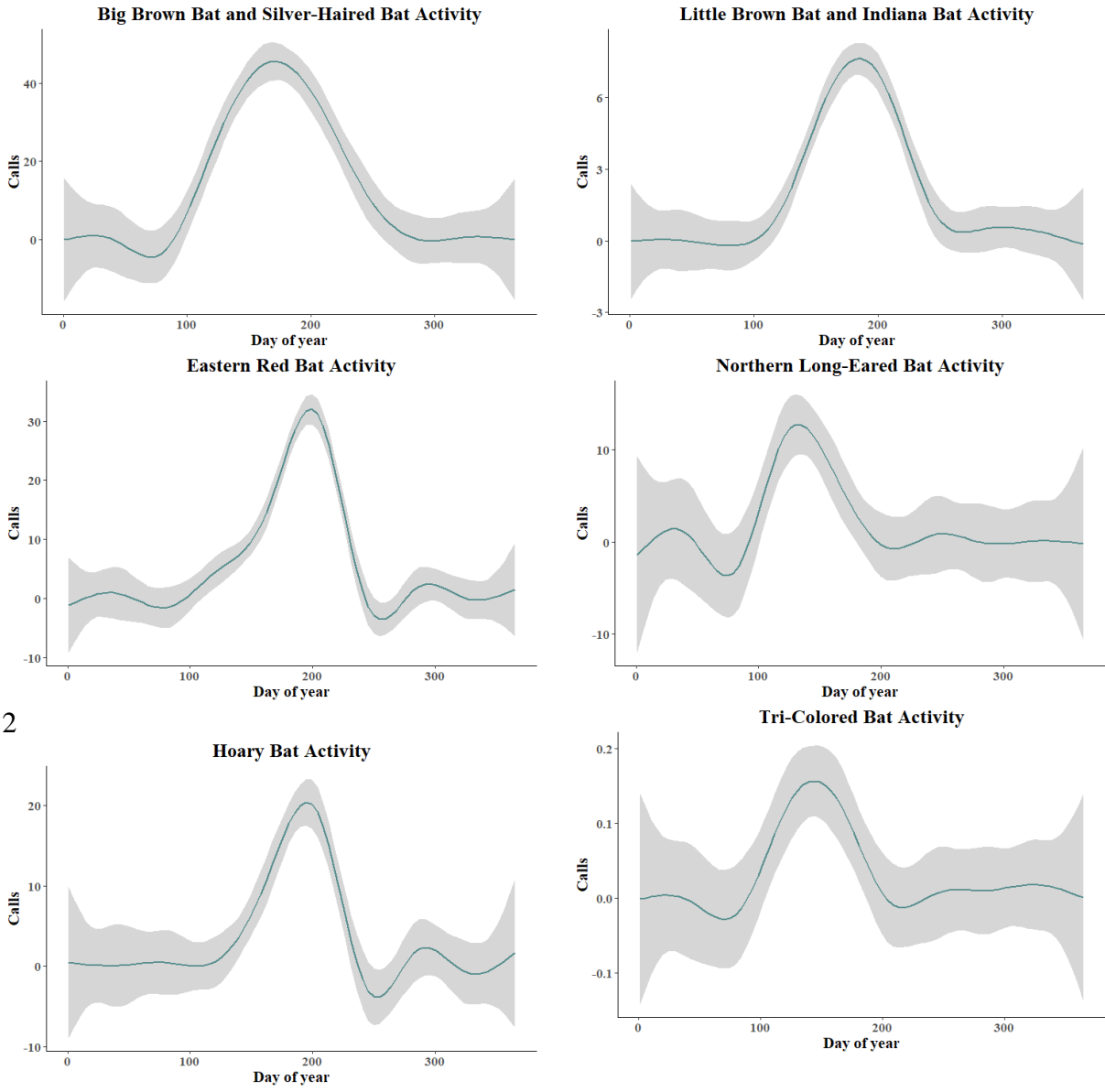


Figure 0-2. Nightly activity patterns for each species/group at the William Floyd Estate, Fire Island National Seashore, New York (Apr 2018–Dec 2019). Raw call file data were smoothed using generalized additive models in order to show seasonal trends; note that y-axes are varied across species/groups. Grey shading is the 95% confidence intervals. Big brown bats (*Eptesicus fuscus*) and silver-haired bats (*Lasionycteris noctivagans*) constitute one phonic group; likewise, little brown bats (*Myotis lucifugus*) and Indiana bats (*M. sodalis*) are combined into one phonic group. Due to the low nightly variation for tri-colored bats (*Perimyotis subflavus*), activity was smoothed according to date and hourly call totals.

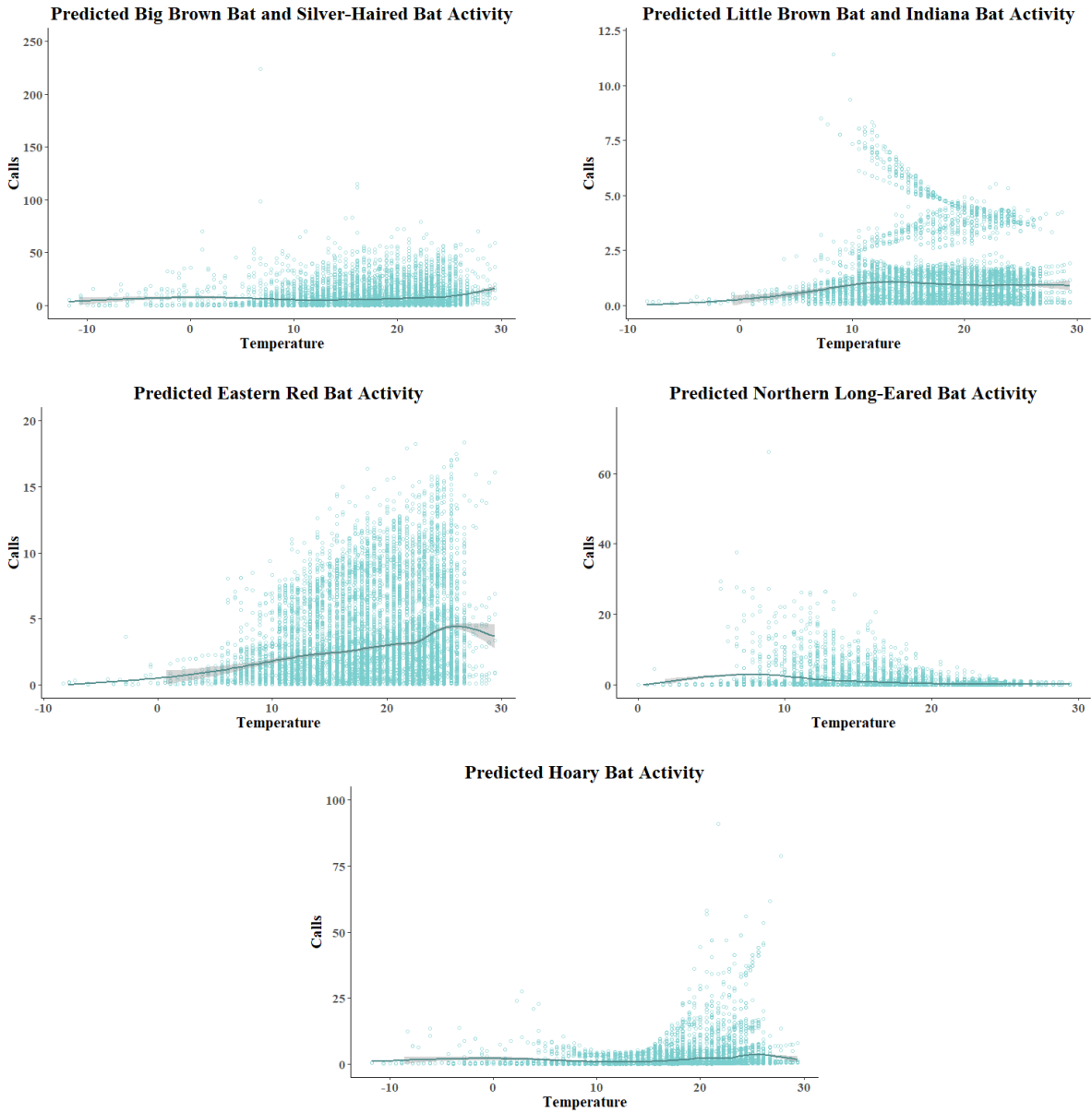


Figure 0-3. Modeled effects on hourly activity for each bat species based on best supported generalized linear mixed models (points), smoothed with generalized additive models for illustrative purposes (blue lines), with 95% confidence intervals (gray), William Floyd Estate, Fire Island National Seashore, New York, maternity season (2018 and 2019). Note the variable x-axes and y-axes across species; x-axes reflect activity window for each species or group. Big brown bats (*Eptesicus fuscus*) and silver-haired bats (*Lasionycteris noctivagans*) were combined into one phonic group; likewise, little brown bats (*Myotis lucifugus*) and Indiana bats (*M. sodalis*) were combined into one phonic group.

Characteristics of day-roosts used by northern long-eared bats (*Myotis septentrionalis*) in coastal New York

Abstract

In North America, northern long-eared bats (*Myotis septentrionalis*) have experienced precipitous declines from White-nose Syndrome. As these bats become rare and difficult to capture, additional day-roost assessments to inform management may fill gaps in our understanding, particularly in habitats and regions where such roosts have never been surveyed. Over two summers, we radio-tracked 16 individuals from a maternity colony on Long Island, NY, in a small forested patch surrounded by development and ocean. These bats disproportionately selected small, suppressed black locusts (*Robinia pseudoacacia*) trees or snags for roosting. Generally, roosts occurred within the interior or edges of this forest patch, rather than surrounding suburbia, reinforcing the hypothesis that northern long-eared bats are forest adapted. Our study shows even small tracts of forest in coastal, urban areas may have conservation value in providing day-roost and foraging habitat.

Introduction

As global diversity of bat species declines due to anthropogenically induced stressors such as habitat loss, degradation, and fragmentation, particularly through urbanization (Thalke et al., 2018), the northern long-eared bat (*Myotis septentrionalis*), a forest-obligate species, faces an additional threat posed by the fungal pathogen *Pseudogymnoascus destructans* that causes White-nose Syndrome (WNS). Since the advent of WNS in North America, the population of northern long-eared bats has declined an estimated >90% throughout 79% of their range (Cheng et al., 2021). Accordingly, in 2012, the Canadian government declared northern long-eared bats as endangered (Forbes, 2012), and subsequently, the species was listed as threatened in New York (New York State Department of Environmental Conservation, 2019) and in the United States (U.S. Fish and Wildlife Service, 2015). Management actions focused on improving, increasing, or generally providing roosting habitat are vital to the survival of remaining colonies on the landscape (Silvis et al., 2016).

Following hibernation, reproductive female northern long-eared bats typically return to the same general areas on the landscape to form maternity colonies and raise their young (Johnson et al., 2012; Perry, 2011; Silvis et al., 2014). Due to their ability to maneuver easily in dense vegetation and glean prey directly from foliage (Faure et al., 1993; Silvis et al., 2016), this species often roosts and forages in mature forest or interior canopy gaps (Bergeson et al., 2021; Divoll et al., 2022; Owen et al., 2002). In

most day-roosting (hereafter roosting) studies, northern long-eared bats preferred cavities to exfoliating bark and snags in increasing stages of decomposition over live trees (Broders and Forbes, 2004; Carter and Feldhamer, 2005; Grider et al., 2021; Menzel et al., 2002; Rojas et al., 2017; Sasse and Pekins, 1996; Silvis et al., 2012). However, local roost preferences are influenced by availability of tree species and forest condition (Perry and Thill, 2007), as well as phase in the female reproductive cycle, which presumably influences selection based on thermoregulatory needs (Drake et al., 2020; Garroway and Broders, 2008; Patriquin et al., 2010; Thalken and Lacki, 2018).

Most studies of roosting by northern long-eared bats have occurred in large, forested landscapes (e.g., Broders and Forbes, 2004; Ford et al., 2016; Johnson et al., 2012; Kalen et al., 2022; Menzel et al., 2002; Perry and Thill, 2007; Silvis et al., 2012). Despite adaptations to forested environments, several observations of northern long-eared bats have occurred post-WNS in fragmented or developed landscapes such as Martha's Vineyard, MA (Dowling and O'Dell, 2018); Washington, DC (Deeley, 2019); and Toronto, ON, Canada (Thorne et al., 2021); as well as in coastal areas formerly believed outside their range (Jordan, 2020; Morris et al., 2009). Individual northern long-eared bats from Long Island, NY, were initially identified and banded in 2015 (Lindsay Ries, U.S. National Park Service, Fire Island National Seashore, NY, 4 March 2019 pers. comm.), and a maternity colony was documented in 2018 (**Nocera 2018**), presenting an opportunity to study roosting preferences of a coastal population in a comparatively urban landscape.

Habitat conditions and year-to-year variation in weather influence roost selection by northern long-eared bats (Patriquin et al., 2016; Perry and Thill, 2007), and examining multi-year roost characteristics across a range of geographic localities is important to inform future regional and localized conservation of the species. Our objective for this study was to characterize maternity roosts and roosting area over two years in a small, fragmented forest surrounded by anthropogenic development and the ocean, which is unlike most previous settings in which research has occurred on day-roosts of northern long-eared bats (Gorman et al., 2022; Silvis et al., 2016).

Northern long-eared bats apparently prefer certain tree species for roosting over others, although selection varies with composition of the local forest (Silvis et al., 2016). For example, in the central Appalachians and Ohio River Valley, if the forest community does not include favored species in abundance, e.g., black locust (*Robinia pseudoacacia*; (Ford et al., 2021; Johnson et al., 2009), northern long-eared bats gravitate to other tree species with similar structural forms and longevity, e.g., sassafras (*Sassafras albidum*; Silvis et al., 2012). If forest composition and structure is less than ideal, these bats may demonstrate even greater plasticity in roost selection on a day-to-day basis, including use of

anthropogenic structures (De La Cruz et al., 2018). We hypothesized that northern long-eared bats on Long Island, similar to those in some other regions, would roost in cavities of black locusts or snags of similar long-standing species (Ford et al., 2006). In addition, we predicted that roosting would occur close to water or other commuting corridors (Divoll et al., 2022; Gorman et al., 2022; Rojas et al., 2017) and within interior forest, rather than in anthropogenic structures in surrounding neighborhoods or forest edges (Thorne et al., 2021). However, we also anticipated some differences in roost selection, relative to previous studies, due to limited availability of older, mature forest on Long Island.

Materials and methods

Study area

We conducted our study on Long Island, New York, at the 248-ha William Floyd Estate (hereafter, the estate) that is part of the Fire Island National Seashore, a unit of the U.S. National Park Service (Figure 0-1). The Atlantic Ocean borders the estate to the south, and the rest is surrounded by urban/suburban neighborhoods. The estate is primarily composed of mature, unmanaged northern coastal oak (*Quercus*)–ericaceous heath forest (65% of total land cover; Gorman et al., 2021; Klopfer et al., 2002). Common tree species are pitch pine (*Pinus rigida*), white oak (*Q. alba*), scarlet oak (*Q. coccinea*), sassafras, black cherry (*Prunus serotina*), red maple (*Acer rubrum*), black locust, and blackgum (*Nyssa sylvatica*). The remainder of the estate consists largely of tidal salt marshes (25%), roads/trails, buildings, and open fields or other areas of sparse vegetation (10%). Average rainfall from May to July is ~10.2 cm; average low temperature during these months is 13.7°C and varies from 8.9°C in May to 17.8°C in July, whereas average high temperature is 23.9°C and varies from 19.4°C in May to 27.8°C in July (U.S. Climate Data, 2020). For a more-detailed description of the local climate, see (Gorman et al., 2021).

Mist-netting and tracking

We conducted mist-netting from 16 May to 26 July 2018 and 15 March to 30 July 2019. We placed mist-netting systems that were 4.8–7.2 m tall and 4–12 m wide (Avinet Research Supplies, Portland, ME) over linear landscape features, such as roads and trails (Deeley, 2019; Silvis et al., 2012). We recorded demographic data including species, sex, age class (adult or juvenile; Brunet-Rossinni and Wilkinson, 2009), reproductive status, and body mass (g) for all captured bats. Upon first capture, we fitted all northern long-eared bats with a uniquely numbered 2.9-mm aluminum alloy band (Porzana, East Sussex, UK) for subsequent identification. We affixed radio-transmitters (0.27 g; model LB-2X; Holohil Systems, Carp, ON, Canada), centered between the scapulae, using a surgical cement (Perma-Type, Plainville, CT). All adult females that were radio-tracked weighed at least 5.4 g, so transmitters were ≤5%

of body mass (Aldridge and Brigham 1988), and a single juvenile male that received a transmitter weighed 6.2 g. All handling of bats followed protocols approved by the Institutional Animal Care and Use Committee of the Virginia Polytechnic Institute and State University, and field work was conducted under the authority of permits issued by the New York Department of Environmental Conservation, U.S. National Park Service, and U.S. Fish and Wildlife Service. We subsequently tracked these bats to roosts using TRX-1000S receivers and matched three-element Yagi antennas (Wildlife Materials, Carbondale, IL) every day for the life of the transmitter, until it fell off or until the bat was not located for three consecutive days. We georeferenced roosts with handheld GPS units (Garmin International, Olathe, KS) and plotted all coordinates in ArcGIS Pro (Version 2.5.0, ESRI, Redlands, CA).

Roost characteristics

We tracked bats during the day, and confirmed occupancy of trees by performing emergence counts every night that a bat with a transmitter was in a roost, weather permitting. During the day following discovery of a new roost, we took measurements of the roost tree and the four closest non-roost trees having a diameter at breast height (DBH) >10 cm as “pseudo-absences”; these were not necessarily true absences, because actual bat use was unknown, but they represented trees that were available to the bats on the landscape (Barbet-Massin et al., 2012; Grider et al., 2021). One non-roost tree was selected in each cardinal direction using the point-quarter method (Jorge et al., 2021). We included species that have not been historically reported as roosts for northern long-eared bats because we questioned whether there were inherent interspecific structural differences among tree species or if northern long-eared bats roost in unlikely species in emergency situations. We used a clinometer (model PM-5/1520; Vantaa, Finland) to measure heights of the roost tree and the emergence points, as well as the height of non-roosts. We measured diameter at breast height with a DBH tape and distance from the roost to each non-roost tree with a tape measure. For each roost and non-roost, we identified species, crown class (1–4: dominant, codominant, intermediate, or suppressed, respectively; Nyland, 2002), and decay stage (1–7: alive, declining, dead, loose bark, clean, broken top, or stump, respectively; Cline et al., 1980). We confirmed whether the emergence point was a cavity or loose bark, recorded the percent bark remaining on the roost, measured the basal area with a 20-factor prism (Forestry Suppliers, Jackson, MS; Thompson et al., 2006), and determined canopy closure using a spherical concave densiometer (Forestry Suppliers, Jackson, MS; Russavage et al., 2021). All means are stated as ± 1 SD.

Statistical analyses

We performed all statistical tests and analyses using R version 4.0.3 (R Core Team, 2020). To compare attributes of roosts versus non-roosts, we made a series of binomial generalized linear mixed models (GLMM; Brooks et al., 2017), with roost versus non-roost as the response variable, total height, DBH, crown class, and decay stage as the predictor variables, and individual roost as the random effect (random trees were assigned the closest roost tree). Prior to model design, we tested for collinearity among our predictor variables using Pearson's correlation coefficient (Wei and Simko, 2021) and found a strong correlation ($>|0.6|$) between only total height and DBH; thus, we did not include those two variables in the same models. We created a set of eight *a priori* candidate models, including a null model and two global models (one with total height and one with DBH). The remaining models were based on our knowledge of the species' ecology and combined structural characteristics (height and crown class, indicating perhaps the amount of solar exposure) with conditional ones (decay stage and DBH, which may influence the internal temperature). We then ranked each model using Akaike's information criteria (AIC) and considered all models within $\Delta\text{AIC} < 2$ to be potentially informative (Burnham and Anderson, 2002). Further, we examined model weights and ecological soundness of top-performing models. We checked each model for goodness-of-fit and over- and under-dispersion in the form of a QQ-plot, residual plot, and a one-sample Kolmogorov–Smirnov test (Hartig, 2020). We evaluated the strength of a predictor variable with a confusion matrix, area under the curve (AUC), and a receiver operating-characteristic (ROC) graph (Sing et al., 2005). The GLMM served as a broad preliminary exploration of differences between trees used as roosts compared to nearby trees that, in theory, were not selected by northern long-eared bats.

To determine if a tree species was used for roosting more or less often than expected based on availability, we performed a Pearson's chi-square test (Venables and Ripley, 2002). We omitted three anthropogenic roosts, a bat house and two wooden utility poles from this analysis, because there were no other ones within the estate, and we also grouped any tree species with less than five observations into a category labelled "other" (Neu et al., 1974). We used $\alpha = 0.05$ as our threshold to determine the significance of the test and used residuals and expected values to determine the relationships between northern long-eared bats and species of trees.

To evaluate landscape characteristics, we collected several spatial attributes relative to roosting locations. We measured the distance from roosts to various types of land cover with the 'Near' tool in ArcGIS Pro. We determined the location of forest and open areas (classes: developed and open space), using the National Land Cover Dataset (U.S. Geological Survey, 2019); water bodies, using the U.S.

Geological Survey National Hydrography Dataset (U.S. Geological Survey, 2020); and roads, using centerline data for Suffolk County, NY (Suffolk County Open Data, 2020), and a roads and trails layer provided by the U.S. National Park Service.

After combining these spatial data with the characteristics of the roost trees (total height of roost, height of bat emergence, DBH, crown class, and decay stage), we performed a principal components analysis (PCA; Oskanen et al., 2020), to assess the whole of roost characteristics from a multivariate approach. We chose PCA as an additional step in our overall analysis to combine numerous, often correlated factors into an interpretable series of wholly orthogonal or independent factors. We selected the first two principal components for visualization (Wickham, 2016), based on examination of proportion of variance explained, eigenvalues, and the screeplot.

Results

In 2018, we captured and affixed transmitters to 14 adult female northern long-eared bats (one of which was banded as an adult in 2015) and tracked them to 21 unique roosts (19 trees, one bat house, and one utility pole). In 2019, we captured and affixed transmitters to three adult females (two of which were banded and tracked as adults in 2018) and one juvenile male. These bats were tracked to 10 unique roosts: one of which was a wooden utility pole that also was used in 2018, an additional wooden utility pole, and eight trees. Across both years, 16 unique individuals were located on 1–10 days each, for an average of 4 ± 2 (SD) days, and followed to 30 unique roosts. In addition to the single juvenile, eight radio-tracked adults were pregnant, seven were of unknown reproductive status (not obviously pregnant, though potentially within early pregnancy), and one was lactating (unknown reproductive status in 2018, but lactating in 2019). Given that reproductive status may have changed during the tracking periods, coupled with the large number of ambiguous reproductive states, we decided to omit reproductive status as a variable in our analysis. After combining data from both years, we calculated a minimum roosting area for the maternity colony of 88.4 ha (Figure 0-1).

Roosts included three anthropogenic structures (two wooden utility poles and one three-chambered traditional bat house) and 10 species of trees, predominantly black locust ($n = 14$; Table 0-1). Non-roost trees were predominantly black locust ($n = 22$) and red maple ($n = 19$) (Table 0-1). For roosts, total height (including anthropogenic structures) was 9.0 ± 4.9 m, roosting height was 4.1 ± 2.0 m, and DBH was 22.5 ± 14.0 cm (Figure 0-2). For non-roost trees, total height was 9.5 ± 7.2 m, DBH was 20.7 ± 12.8 cm (Figure 0-2), and distance to the roost tree was 5.4 ± 5.4 m. Crown classes of roosts trees were mostly codominant or suppressed (34% and 41%, respectively) and evenly distributed across all decay

stages, with the exclusion of stump (Table 0-2). Most non-roost trees were alive (64%), and approximately one-third (36%) were suppressed. Roosts were located 44.0 ± 34.3 m from the nearest road, 268.8 ± 185.4 m from fresh water or tidal streams, 4.7 ± 14.2 m from forest (23 roosts within forest, six outside forest), and 25.3 ± 30.6 m from the nearest open field (Figure 0-3).

Our top-performing GLMM had a model weight of 0.73 and included decay stage and crown class individually and as an interactive term, with no other model coming within two Δ AIC units (Table 0-3). Alone, crown class was not a significant predictor in roost selection (confidence intervals crossed zero), whereas decay stage alone had a statistically significant positive relationship with roost selection (confidence intervals did not cross zero), but for the two variables combined, there was a negative relationship with roost selection (confidence intervals did not cross zero; Table 0-4).

Our Pearson's chi-square revealed a relationship between roost species and use by northern long-eared bats ($\chi^2_8 = 18.3$; $n = 132$; $p = 0.02$; Table 0-5). Snags not identified to species and black locusts were used significantly more often than expected based on availability, and all other species were used equitably or slightly less often than expected (Table 0-5).

From our PCA, the first three components combined for 69.4% of variance in roost characteristics, with the first, second, and third components explaining 35.5%, 20.5%, and 13.4%, respectively (Table 0-6). The first component was most representative of general roost characteristics and had high loadings of total roost height (1.10), DBH (1.09), and distance to water (-0.97). The second component was primarily representative of decay stage (-0.96) and crown class (-0.86), whereas the third component represented distance to road (0.86) and basal area (-0.70). Our PCA identified clear clustering in roost characteristics among black locusts, with red maples and snags often falling on the opposite side of the graph, meaning black locust was favorable for one combination of variables, whereas red maple and snags were favored under opposite circumstances (these three trees were the species most commonly used as roosts; Figure 0-4). There was a strong association with use of short, low-DBH black locusts with increased distance to water, which was the opposite for blackgum and, to a lesser extent, red maple. As the basal area (a surrogate for clutter or stem density) increased, there was a strong association of snag use.

Discussion

A roosting area of 88.4 ha for the maternity colony on Long Island was more than that observed in studies in Canada, West Virginia, Kentucky, and Wisconsin (min–max = 0.39–58.5 ha; (Henderson and Broders, 2008, p. 20; Hyzy et al., 2020; Johnson et al., 2012; Silvis et al., 2015a). Smaller roosting areas could reflect short tracking periods (i.e., if bats were not followed long enough to identify the entire scope of their inter-roost movements) or result from “condensed” but superior habitat in terms of roost availability and foraging conditions (Ford et al., 2016; Johnson et al., 2012, 2009). In our study, despite tracking periods on par with other studies, the larger roosting area may reflect poor roosting and foraging habitat within and around the estate.

Although other studies have shown that northern long-eared bats occasionally roost in anthropogenic structures, those structures typically were located within or on the edge of forested habitat (De La Cruz et al., 2018; Dowling and O’Dell, 2018; Henderson and Broders, 2008). Despite the abundance of anthropogenic structures that could double as roosts in the surrounding urban area of Long Island (e.g., houses and wooden utility poles), we found no evidence to suggest that the bats of this colony moved far from the forests at the estate; the bat house was the only roost outside the forest, but it was located 79 m from the edge. The closest patches of woodland, other than trees associated with anthropogenic structures outside the estate, were >3 km beyond neighborhoods to the west in the Wertheim National Wildlife Refuge or >1 km to the south over open ocean on Fire Island. Although we cannot say definitively that members of this colony were limited to the estate, we did not note any movements to the available forests to the west or south during our tracking. Though variable with numerous instances to the contrary, most research has shown that the combined roosting and foraging range of female northern long-eared bats is <300 ha (Broders et al., 2006; Johnson et al., 2012; Owen et al., 2003), further suggesting that movement to the west or south to Fire Island is unlikely, based on both distance and habitat unsuitability.

The colony’s use of the estate and avoidance of surrounding areas likely is related to several factors. First, there is less artificial light within the forest at the estate, and increases in light pollution typically decrease bat activity (Rowse et al., 2016) because of increased predation risk and decreased prey diversity and abundance (Threlfall et al., 2012; Villarroya-Villalba et al., 2021). Second, constant vehicular traffic may be an additional deterrent (Thorne et al., 2021). The density of human development (and thus light pollution and traffic) surrounding the estate could serve to concentrate prey, forcing northern long-eared bats to forage within the forest or along its edge. This hypothesis is supported by an acoustic analysis at the estate, which noted that activity of northern long-eared bats was highest within

forested patches and edges (Gorman et al., 2022). The estate forms a tract of forested land that is geographically isolated from similar habitat, thus providing a terrestrial, “island” refugium, and potentially indicating that the area contains at least the minimum requirements for a successful maternity colony. The Atlantic Ocean serves as an additional natural barrier to movement and also creates highly variable weather conditions that may necessitate numerous roosts with differing structural characteristics and microclimates to accommodate changing physiological needs throughout the maternity season.

Height and DBH were comparable between roosts and non-roost trees in our study, pointing to no superficial structural differences between the two groups other than roosts tended to be more advanced in the decay process than random trees. This finding is congruent with other studies of roosting by northern long-eared bats that have shown a preference for snags versus live trees (Carter and Feldhamer, 2005; Grider et al., 2021; Rojas et al., 2017; Silvis et al., 2012). Our mean DBH is comparable to the diameter of maternity roosts of northern long-eared bats in coastal North Carolina (20.6 cm; Jordan, 2020) but much less than the mean DBHs from studies at inland and montane sites (31.1–65.0 cm; (Broders and Forbes, 2004; Carter and Feldhamer, 2005; Foster and Kurta, 1999; Grider et al., 2021; Rojas et al., 2017; Silvis et al., 2015b). Moreover, because the relationship between selection and decay stage was reversed when crown class was added as an interactive term, we found evidence for selection of snags in lower crown classes, similar to Johnson et al. (2009). Our beta value was lower for the interactive term as compared to decay stage alone; therefore, it is likely that this relationship is an artifact of the selected roosts being evenly distributed across the crown classes (tempering the strong positive effects of decay stage). The PCA further highlighted use of shorter and thinner (low DBH) black locusts in areas of high-clutter and shade, which is opposite the typical pattern of large tall trees with high solar exposure reported for other species (Barclay and Kurta, 2007) but consistent with the GLMM results.

When we compared across tree species for roost use, the significant residuals further confirmed black locust and unidentified snags in use more often than expected based on their availability among our random sample of trees. The demonstrated longevity, hardness, and rot-resistance of black locust (Adams and Owens, 2001; Cuno, 1930; Ford et al., 2006; Meier, 2022), coupled with its reputation for cavity formation (Carey et al., 1983; McComb and Muller, 1983), may make it the ideal roost for the species, as its presence may be dependable year after year, and there may be several cavity options on the bole itself. Other studies of maternity roosts of northern long-eared bats reported a selection for black locust, particularly in areas where it was abundant (Ford et al., 2006; Hyzy et al., 2020; Johnson et al., 2009; Menzel et al., 2002; Owen et al., 2002). The clustering of black locust directly opposite other species on the PCA plots suggests that female northern long-eared bats identify and may be selecting specific roosts that provide optimal thermoregulatory conditions (Garroway and Broders, 2008; Patriquin et al., 2010;

Silvis et al., 2015a; Thalken and Lacki, 2018). Within the context of our study, thermoregulatory needs could have been dictated by reproductive status (Garroway and Broders, 2008; Patriquin et al., 2010; Silvis et al., 2012), maritime-influenced weather (Gorman et al., 2021), some combination of these two variables, or other factors entirely.

Despite distance to water having a strong association with roosts, it seems that the association was largely species-based, with black locusts falling mostly on one side of the PCA and all other species scattered on the opposite end. This result could reflect the specific habitats where those tree species are found (some trees are more common in the marshy areas of the estate) and that northern long-eared bats base their roost selection on environmental cues coupled with their thermoregulatory needs. Further research with larger sample sizes, more diversity in reproductive stages, and longer tracking periods are needed to explore the mechanisms behind these patterns and how they might be similar to or differ from better-studied inland populations.

Our research at the estate provides additional insights into the post-WNS roosting ecology of northern long-eared bats in a coastal and urbanized setting. Much like northern long-eared bats in an urban forest in Toronto (Thorne et al., 2021), the population at the estate made little use of the anthropogenic environment around them, further highlighting the importance of conserving heterogeneous forest patches for bats, even in areas of high human occupancy. Whereas some aspects of roost selection and use differed from previous research at inland sites, roosting ecology of northern long-eared bats on Long Island generally conformed to that of inland locations. Given the post-WNS rarity of northern long-eared bats throughout their distribution along with the paucity of roosting data from urban and coastal areas, the observations we made may be useful to inform species-specific conservation protocols going forward. Whether or not coastal populations, such as the one we studied, are unaffected by WNS and are successfully reproducing is unknown, but our findings may assist resource personnel with identifying and managing other areas in the coastal Northeast with potential suitable and perhaps occupied habitat. In addition, our study shows even small tracts of forest in coastal, urban areas may have conservation value in providing day-roost and foraging habitat.

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Tables

Table 0-1. Total counts of roost types and non-roost tree species used by northern long-eared bats (*Myotis septentrionalis*) at the William Floyd Estate, New York (2018–2019).

Species or type	Total roosts (2018/2019)	Non-roost trees
Norway Spruce ^a	0	1
Redcedar ^a	0	2
Hickory	1 (1/0)	9
White Oak ^a	1 (0/1)	3
Bear Oak ^a	0	2
Northern Red Oak	1 (1/0)	11
American Elm ^a	0	2
Sassafras ^a	0	1
Spicebush	0	6
Black Cherry	0	12
Black Locust	14 (13/1)	22
Red Maple	4 (3/1)	19
Blackgum	2 (0/2)	10
Eastern Persimmon ^a	1 (0/1)	2
Unidentified snags	3 (1/2)	4
Bat house ^c	1 (1/0)	0
Wooden utility poles ^c	2 ^b (1/2)	0
Total	30^b (21/10)	106

^a Species denoted as “other” for Pearson’s chi-square analysis.

^b One wooden utility pole was used in both years but is quantified as one roost.

^c Anthropogenic structures were omitted from Pearson’s chi-square analysis.

Table 0-2. Crown class and decay stage for roosts and non-roosts of northern long-eared bats (*Myotis septentrionalis*) at the William Floyd Estate, New York (2018–2019). Numbers in brackets refer to crown class and decay stage designations in models.

Crown class	Roosts	Non-roosts
Dominant [1]	6	20
Codominant [2]	10	27
Intermediate [3]	1	21
Suppressed [4]	12	38
Decay stage		
Alive [1]	6	68
Declining [2]	4	9
Dead [3]	4	5
Loose bark [4]	6	8
Clean [5]	4	3
Broken top [6]	5	11
Stump [7]	0	2

Table 0-3. Akaike’s information criteria (AIC) table showing all models testing relationship of roost selection by northern long-eared bats (*Myotis septentrionalis*) at the William Floyd Estate, New York (2018–2019) to roost variables, AIC score, delta AIC, and model weights (ω_i); an * denotes an interaction. Predictor variables included crown class, decay stage, height of potential or actual roost in meters (height), and diameter at breast height (DBH) of potential or actual roost. Roost ID was included in all models as a random effect.

Model	AIC	Δ AIC	ω_i
Crown class * decay stage	128.75	0.00	0.73
Height * decay stage	133.09	4.34	0.08
DBH + crown class + decay stage	133.32	4.56	0.07
Height + crown class + decay stage	133.58	4.82	0.07
Height + decay stage	134.60	5.85	0.04
Null model	138.97	10.22	<0.01
Height + crown class	142.48	13.73	<0.01
DBH + crown class	142.76	14.01	<0.01

Table 0-4. Predictor variables, beta (β) values, standard errors (SE), lower (LCL) and upper (UCL) 95% confidence intervals for top model output of roost selection by northern long-eared bats (*Myotis septentrionalis*) at the William Floyd Estate, New York (2018–2019) related to roost variables; an * denotes an interaction.

Predictor variables	β	SE	LCL	UCL
Crown class	0.21	0.38	-0.54	0.97
Decay stage	1.35	0.49	0.38	2.32
Crown class * decay stage	-0.28	0.14	-0.56	-0.01

Table 0-5. Standardized Pearson’s residuals and expected values for chi-squared analysis, comparing species of non-roost and day-roost trees used by northern long-eared bats (*Myotis septentrionalis*) at the William Floyd Estate, New York (2018–2019). Residual values close to |2.00| are considered influential (indicated by †; Silvis et al. 2015b). Negative and positive values indicate lesser and greater abundance than expected, respectively. “Other” includes: Norway spruce (*Picea abies*), Eastern redcedar (*Juniperus virginiana*), white oak (*Quercus alba*), bear oak (*Q. ilicifolia*), American elm (*Ulmus americana*), sassafras (*Sassafras albidum*), and Eastern persimmon (*Diospyros virginiana*).

Tree species	Residuals		Expected		Use vs. availability
	Roost	Random	Roost	Random	
Hickory (<i>Carya</i> spp.)	-0.69	0.34	1.97	8.03	Lesser
Northern red oak (<i>Quercus rubra</i>)	-0.89	0.44	2.36	9.64	Lesser
Spicebush (<i>Lindera benzoin</i>)	-1.09	0.54	1.18	4.82	Lesser
Black cherry (<i>Prunus serotina</i>)	-1.54	0.76	2.36	9.64	Lesser
Black locust (<i>Robinia pseudoacacia</i>)	2.33†	-1.15	6.89	28.11	Greater
Red maple (<i>Acer rubrum</i>)	-0.64	0.32	4.33	17.67	Lesser
Blackgum (<i>Nyssa sylvatica</i>)	-0.24	0.12	2.36	9.64	Lesser
Other	-0.56	0.28	2.95	12.05	Lesser
Snag	1.93†	-0.96	1.56	6.42	Greater
χ^2	18.33				
p-value	0.019				

Table 0-6. Principal components analysis of characteristics of day-roosts used by northern long-eared bats (*Myotis septentrionalis*) at the William Floyd Estate, New York (2018–2019).

	Principal component 1	Principal component 2	Principal component 3
Eigenvalue	4.26	2.46	1.60
Proportion explained	0.355	0.205	0.134
Cumulative proportion	0.355	0.561	0.694

Figures

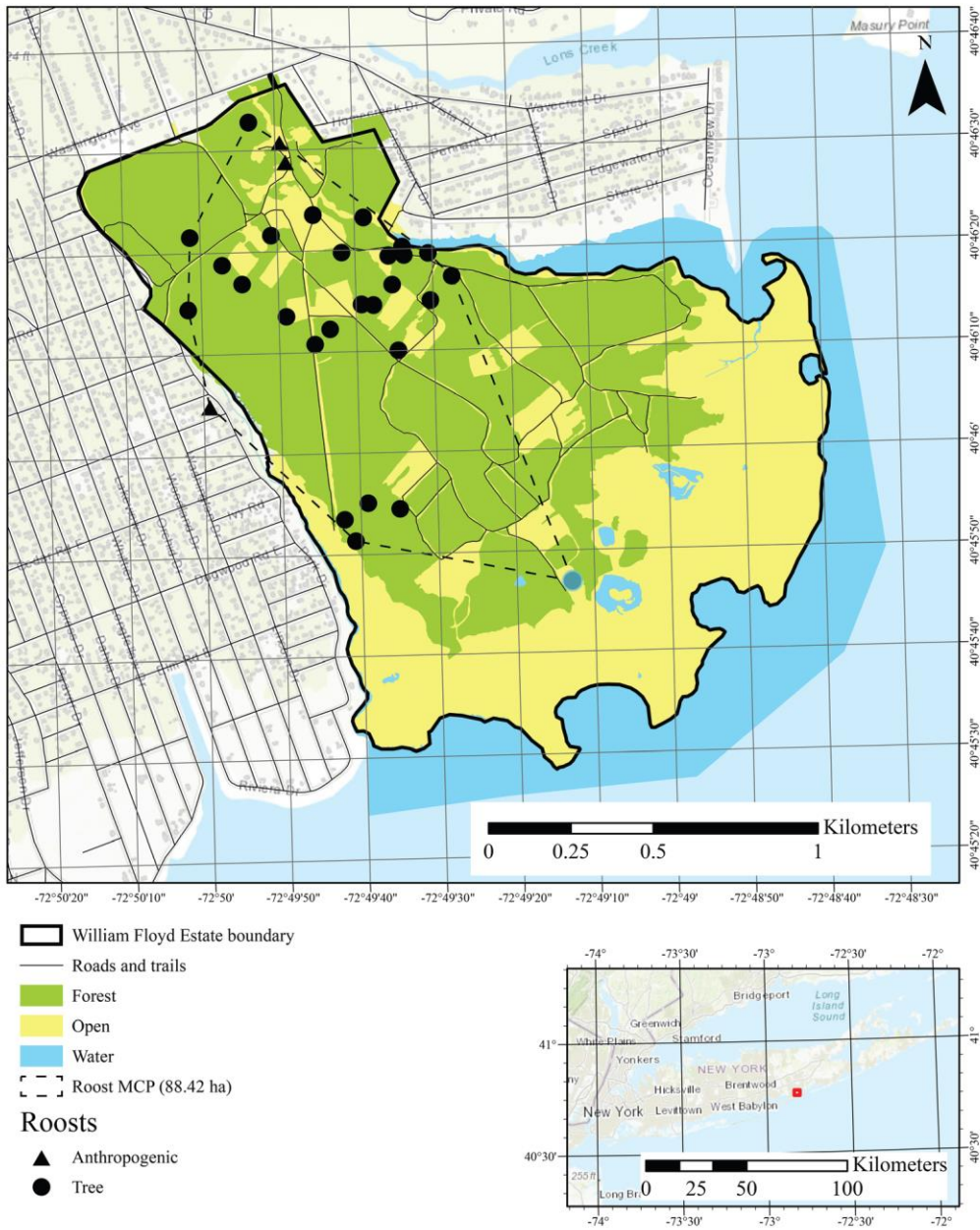


Figure 0-1. Map of roosts used by northern long-eared bats (*Myotis septentrionalis*) at the William Floyd Estate, New York (2018–2019). Roost MCP is a minimum convex polygon defining minimum roosting area over both years combined. Red rectangle on the inset map (ESRI, Redlands, California) indicates study area.

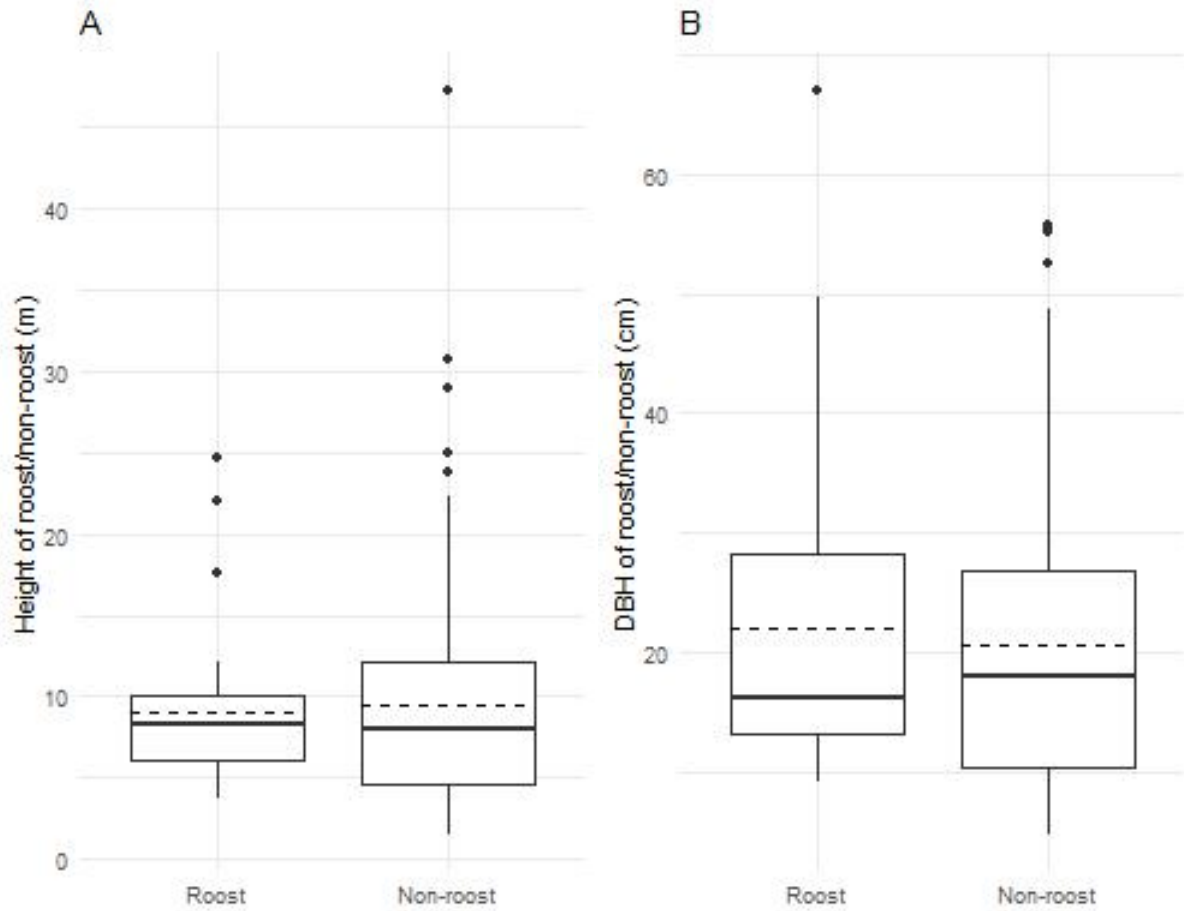


Figure 0-2. Boxplots of height (A) and diameter at breast height (DBH; B) for summary data of roosts used by northern long-eared bats (*Myotis septentrionalis*), including anthropogenic structures, and non-roost trees. Dashed lines represent means, dots represent outliers, tails represent 95th percentile, box bounds represent 50th percentile, and solid lines in boxes represent median values.

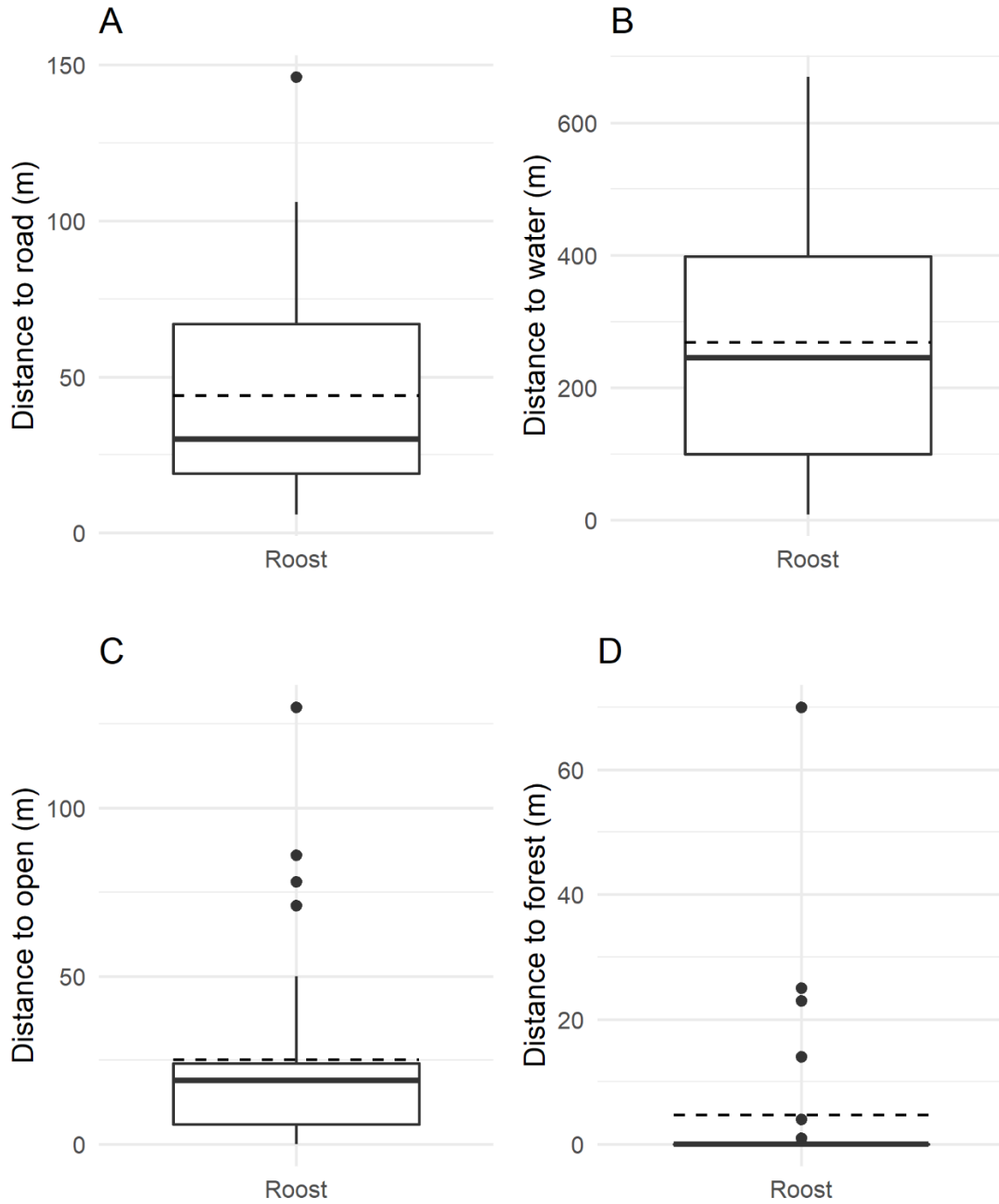


Figure 0-3. Boxplots of distance to road (A), water (B), open (C), and forest (D) for roosts used by northern long-eared bats (*Myotis septentrionalis*), including anthropogenic structures. Dashed lines represent means, dots represent outliers, tails represent 95th percentile, box bounds represent 50th percentile, and solid lines in boxes represent median values. Note the varying y-axis values.

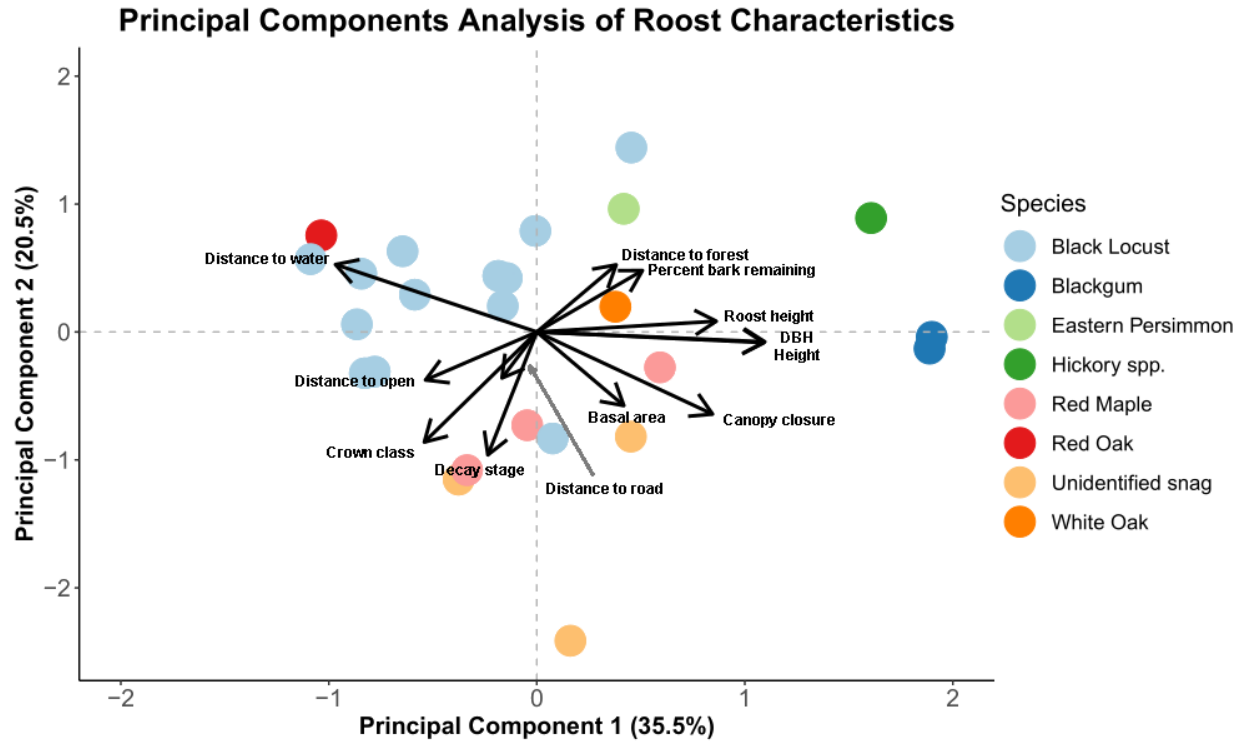


Figure 0-4. Principal components 1 and 2 for roosts used by northern long-eared bats (*Myotis septentrionalis*) at the William Floyd Estate, New York (2018–2019). Arrow lengths indicate effect size. Direction of arrow relative to species points indicates positive or negative relationship. For example, in this figure, there is a positive relationship with black locust (*Robinia pseudoacacia*) as distance to water increases. There is a negative relationship with black locust as canopy closure and height increase. Diameter at breast height (DBH) and height arrows overlap. See text for scientific names of tree species in figure legend.

Network analysis of a northern long-eared bat (*Myotis septentrionalis*) maternity colony in a suburban forest patch

Abstract

Many bat species are highly social, forming groups of conspecifics, particularly during the maternity seasons. In temperate North America, these social groups are typically comprised of closely-related individuals or individuals that share some common trait (i.e., reproductive state or shared hibernacula from the previous winter). In the summer, when bats use forests for day-roosts, these social groups often demonstrate nonrandom patterns of periodically associating in common roosts and disassociating using different roosts as a “fission–fusion society”. As hibernating bat species in North America continue to decline due to the impacts of White-nose Syndrome, opportunities to describe these dynamics are becoming rare. Unfortunately, these patterns often are still poorly understood, yet these are critical information components for habitat conservation and management. In our study, we tracked female northern long-eared bats (*Myotis septentrionalis*) to their day-roosts in a small, suburban forest fragment in coastal New York, USA, in the summers of 2018 and 2019. We confirmed that the bats shared roost sites and, using network analyses, we analyzed social dynamics and space use. In contrast to previous research on this imperiled species in large, unfragmented core forests, we found a denser and more connected roost network that concentrated around forest patch edges. Unusual for this species, primary roosts were humanmade structures. Our findings suggest that northern long-eared bats can utilize small forest patches and that incorporation of anthropogenic roosts might be an effective strategy for long-term conservation in more urbanized landscapes where forest management actions to enhance day-roosting conditions are impractical and the risk of stochastic loss of roosts is high.

Introduction

Communal roosting is common among North American Vespertilionid bats throughout the year, with seasonal variation in social structures of those groups (Kerth, 2008a). In the winter, many cave- and mine-hibernating bats cluster together in predominantly single-species aggregations (Davis, 1970). In the summer, reproductive females will often further subdivide into colonies that are sometimes related along matrilineal lines (Kerth, 2008b; Patriquin et al., 2013; Silvis et al., 2014b; but see Olivera-Hyde et al. 2019).

Social roosting in bats allows allonursing and communal rearing of young, thermoregulatory benefits, and information transfer (Kerth, 2008a; Silvis et al., 2014b). However, one major disadvantage to communal roosting is the greater potential for disease transmission among conspecifics (Johnson et al., 2012; Kerth, 2008a). For the hibernating bats of North America, this is a contributory factor for the spread of White-nose Syndrome (WNS), a disease caused by the invasive fungal pathogen *Pseudogymnoascus destructans* (Cheng et al., 2021). As a result, communal roosting has resulted in population declines of >90% of several temperate zone hibernating bats in North America (Cheng et al., 2021; Powers et al., 2015).

During the summer months In North America, several species of bats form maternity colonies in which frequent roost switching is well documented (Silvis et al. 2016): bats from a larger group will sporadically disassociate into smaller groups (mother/juvenile pairs) and use secondary roosts, and then periodically return to primary colonial roosts. This type of roost switching behavior is a characteristic of fission–fusion societies. Fission–fusion dynamics are present in many bat species (Johnson et al., 2012; Kerth and König, 1999; Patriquin et al., 2010; Silvis et al., 2014b; Willis and Brigham, 2004). Network analyses often have been used to describe these fission–fusion patterns in bats (Chaverri, 2010; Johnson et al., 2012; Kerth, 2008b; Patriquin et al., 2010; Silvis et al., 2014b), allowing researchers and managers to get a better understanding of how the colony uses and moves around the landscape, and to identify sources of weakness in the structure of the society.

The federally threatened northern long-eared bat (*Myotis septentrionalis*) is one of the bat species in eastern North America that displays a fission–fusion dynamic during the temperate summer maternity season (Garroway and Broders, 2007; Patriquin et al., 2010; Silvis et al., 2014a). As northern long-eared bats have experienced substantial population declines due to WNS, several studies have used network analysis metrics to describe their roost-switching patterns and inter-individual relationships, and to better understand habitat and roosting needs of this species. These studies have been conducted in largely closed-canopy, contiguous forests usually with the potential for an abundance of available roosts across an expansive spatial extent. Regardless of geographic locale, patterns emerged among most colonies: communal node trees were identified and bats had preferred one to two roosting companions when they disassociated from the larger colony ranging from 12–88 individuals (Garroway and Broders, 2007; Johnson et al., 2012; Owen et al., 2002; Patriquin et al., 2010; Silvis et al., 2014a).

In this study, we explored the social dynamics of a post-WNS maternity colony in a comparatively more developed, coastal landscape in the northeastern United States. Due to their volant nature with high vagility, in theory, bats may be less constrained by habitat extent and connectivity than

other terrestrial species. However, the demonstrated importance of social and familial relationships coupled with demonstrated multi-year roost fidelity of northern long-eared bats may negatively affect individual dispersal or fusion of multiple colonies, particularly in an area with limited natural resources and small, disconnected forest tracts. In recent years, researchers have been finding northern long-eared bats in comparatively patchier, more urban landscapes than what has previously been recorded for the species (Deeley, 2019; Hoff et al., In review; Thorne et al., 2021). With northern long-eared bats maintaining social connectivity and reproductive success, even in areas with patchy forest, understanding these populations could inform adaptive management going forward (Finch et al., 2022; Rhodes et al., 2006; Snijders et al., 2017).

We hypothesized that a northern long-eared bat maternity colony in a highly-developed landscape would still display a general fission–fusion structure. However, given the more constrained, isolated nature of our study area and reduced populations from WNS, we thought the colony would be more centralized with fewer connections (nodes) than work from larger forested landscape pre-WNS, that there would be stronger connections between bats, proportionally more use of primary (high-density) roosts, and less use of secondary roosts. Further, we hypothesized that while constrained overall by the small residual forest patch size, bats in this post-WNS colony would have a larger roost-area spatial footprint than observed in previous studies.

Materials and methods

Study area

Our study was conducted at the William Floyd Estate (hereafter, the Estate), a 248-ha coastal park on the southern shore of eastern Long Island, New York, USA, managed by the National Park Service (Figure 0-3). It is located approximately mid-way between the northernmost and southernmost portions of the northern long-eared bat’s coastal distribution (Grider et al., 2016). Much of the Estate land is comprised of unmanaged, second- or third-growth oak (*Quercus* spp.)-dominated forest (65% of the Estate area in total) interspersed with open fields and salt marsh, breaking the forest into several small patches (for a more detailed description see Gorman et al., 2022; Klopfer et al., 2002). Located approximately 100 km east of New York City, the Estate is surrounded by dense suburban neighborhoods to the north and west, and the Atlantic Ocean to the south and east. Outside of the Estate, bats would need to fly a minimum of 3 km to the east or west to reach additional forested habitat without having to cross

open ocean, a distance greater than most observed mid-summer movements for northern long-eared bats (Henderson and Broders, 2008). Long Island is frequently impacted by severe coastal weather events; however overall, the climate is moderated by maritime influences, i.e., milder winters and cooler summers than what interior New York State experiences (Gorman et al., 2021).

Field work

We caught bats from May–June 2018 and May–July 2019 using 4–12 m length, 38 mm bat mist-nets (Avinet Research Supplies, Portland, ME, USA) in single-, double-, and triple-high configurations over wooded roads and trails throughout the Estate (Deeley, 2019; Gorman et al., 2022; Silvis et al., 2012). After recording sex, age class (based on epiphyseal gap; Brunet-Rossinni and Wilkinson, 2009), and weight, we fitted all northern long-eared bats with a uniquely-numbered aluminum alloy band (Porzana Ltd., Icklesham, East Sussex, United Kingdom). For subsequent radio-tracking, we affixed Holohil LB-2X VHF radio transmitters (0.27 g, lifespan 8–15 days; Holohil Systems Ltd., Carp, Ontario, Canada) between the scapulae with surgical cement (Perma-Type Company Inc., Plainville, CT, USA) to all adult female northern long-eared bats and one juvenile male (6.2g; Gorman et al., 2022b; Silvis et al., 2014a) following the 5% rule (transmitters must not exceed <5% of the bat’s body mass; Aldridge and Brigham, 1988). We tracked radio-tagged bats to their day-roosts using TRX-1000S receivers and folding three-element Yagi antennas (Wildlife Materials Inc., Carbondale, IL, USA) for the life of the transmitter, until it fell off, or until the bat could no longer be located three days in a row in the Estate or within 1.5 km of the boundary. When a roost was located, we georeferenced it with handheld GPS units (Garmin International Inc., Olathe, KS, USA). To maximize our potential of catching and radio-tagging bats within the same colony, we erected mist-nets around the located roost when cavities or loose bark were at or below the height of our triple-high net poles (approximately 7 m). Aberrant day-roosts such as utility poles were not netted for safety reasons. If weather permitted, we performed nightly emergence counts on each roost (Foster and Kurta, 1999) to assess colony size.

Network analysis

We calculated distance between subsequent roosts using the *sp* and *adehabitathR* packages (Calenge, 2006; Pebesma and Bivand, 2005) in R (version 4.0.3; R Core Team, 2020). We created a utilization distribution using a fixed kernel method to approximate space use by the colony. To generate a more realistic representation of the space use area relative to the intensity and concentration of roost use, we weighted each roost location by the number of days the roost was used and added anonymous bats to reflect the emergence count numbers on those days (Popa-Lisseanu et al., 2008; Silvis et al., 2014b). We

used base Program R to calculate summary statistics for day-roosts: mean number of tracking days per bat, mean number of roosts used by each bat, mean relocations, individual bat roost switching frequency, and the number of times each roost was used throughout the tracking periods.

To characterize colony structure at the individual and community levels despite our disparate tracking periods, we used the *igraph* (Csardi and Nepusz, 2006) and *tnet* (Opsahl, 2009) packages. We then projected the two-mode network (bipartite, bat to roost) into two one-mode networks (unipartite, bat to bat and roost to roost). To describe network coherence, we calculated the mean degree, the degree centralization index, and the betweenness centrality index. Degree describes the distance between the nodes based on the number of other nodes with which they are in direct contact, and is a measure of connectivity and centrality (Dong and Horvath, 2007; Freeman, 1978). The degree centralization index and betweenness index are methods that use the node-level centrality scores to measure the difference between the node(s) with the most connections (degree) and the number of nodes that fall between two others (betweenness) against the centrality scores of rest of the group; these indexes range in value from 0 (low) to 1 (high; Freeman, 1978). We used the UCINET software (Borgatti et al., 2002) to explore the same network measures exclusive of betweenness to create visualizations. We assessed the structures of the networks by calculating network densities, and calculated clustering for the entire bipartite network. This clustering measures how densely-packed or “cliquish” the connections and nodes are and the degree whereby individual bats are known to one another (Dong and Horvath, 2007; Opsahl, 2013; Opsahl and Panzarasa, 2009). We calculated clustering as a scaled 0 (low) to 1 (high) value following Silvis et al. (2014b).

Results

Over both summers, we captured 20 individual northern long-eared bats ($n = 16$ total captures in 2018 and $n = 6$ total captures in 2019, including two recaptures). In 2018, one captured adult female had been banded during earlier monitoring efforts from 2015 and two bats were unable to be tracked. Captures were higher in 2018 because we were able to put transmitters on eight bats in one night while netting the bat house. In 2019, two adult females from 2018 were recaptured, as well as a new juvenile male and female, and one adult male that was not tracked. Of the juveniles, only the male was large enough to receive a transmitter. From the 16 individuals with transmitters, we documented 30 unique day-roosts – one of which was a utility pole used both years. Three of the recorded day-roosts were anthropogenic structures (one bat house and two utility poles; Figure 0-1 & Figure 0-2), the remaining

were live trees or snags of eight species or snags for which we could not determine species (Gorman et al., 2022a). All day-roosts we located were within the Estate boundary, with the exception of the bat house that was located at a private residence approximately 80 m east of the Estate boundary. Twenty-one (ca. 70%) of these day-roosts were snags or declining live trees (Gorman et al., 2022a), six trees were alive, and the three anthropogenic roosts were not assigned a decay stage. Twenty-two emergence counts accounted for 1–11 exiting bats per roost on any given night. The mean distance traveled between roosts was 228.3 m ($SD \pm 307$ m, range 0–1233.09; Table 0-1) for all tracked bats; for bats restricted to the connected network, the mean distance travelled between roosts was 238.4 m ($SD \pm 311.6$ m, range 0–1233.09). The Utilization Distribution displayed two noticeable core areas that were centered around the bat house and utility poles used as roosts for multiple bats over multiple days, and estimated 95% utilization distribution of 135.09 ha (Figure 0-3). In a previous study, a minimum convex polygon encompassing the roosts measured 88.4 ha (Gorman et al., 2022a).

Our one-mode network visualizations initially revealed that two bats were not connected to the larger network (the juvenile male and one adult female from 2019), so the only tracked bats from 2019 retained in the network analysis were the recaptures from 2018. Our final network for the analysis consisted therefore of 14 bats, 25 roosts, and 45 connections between bats and roosts (Figure 0-4). On average, bats were tracked for 4.4 days each year ($SD \pm 2$, range 1–10), regardless of whether or not they were connected to the colony. Over both years, bats in the connected network used a mean of 3.2 day-roosts ($SD \pm 1.7$, range 1–6), had 5.07 ($SD \pm 3.4$, range 1–17) relocations, and displayed a roost-switching frequency of 1.5 days ($SD \pm 0.5$). Each roost was used, on average, 2.73 ($SD \pm 3.9$) times. Mean degree of the bat network was 9.57, and the degree centralization index was 0.31 (no individual bats were driving the connectivity). The betweenness index was 0.87 (many bats are connected through other bats) and density was 0.74 (see Figure 0-5 for unipartite networks). The roost network mean degree was 4.88. The centralization and betweenness indices were 0.55 and 0.47, respectively (individual roosts were more important to connectivity and they were more directly connected to one another), and the network density was 0.20. Clustering over the entire network was 0.12 (low frequency of distinct cliques).

Discussion

Our study examined roost and social network patterns for a northern long-eared bat maternity colony over the course of two years in a small, coastal forest fragment surrounded by dense suburban development and the ocean. Although single- and multi-year analyses of maternity networks have been

conducted for this species previously, these occurred either before the local introduction of WNS or at the beginning of the disease advent prior to large local to regional population declines (Ford et al., 2016; Foster and Kurta, 1999; Garroway and Broders, 2008; Hyzy et al., 2020; Patriquin et al., 2010; Sasse and Pekins, 1996; Silvis et al., 2014a). Similar to other northern long-eared bat maternity studies, we confirmed ongoing site – and further, roost-specific – philopatry with recaptures of banded bats across years (Olivera-Hyde et al., 2019; Patriquin et al., 2010; Perry, 2011). This continued pattern suggests that at least through 2019, despite disruptions to the overall population, northern long-eared bats were continuing to form colonies, albeit of reduced size, in their natal area *or* persisting northern long-eared bat females were joining existing colonies to cope with their own colonies' collapses as posited by Kalen et al. (2022).

Our minimum colony size (not including juveniles) was 15 bats, based on the total number of unique adult females we tracked over the two years. It is unlikely we were able to capture every colony member, but our low emergence count numbers compared to other studies indicate a smaller overall colony size than perhaps would have existed prior to WNS, though colony sizes for northern long-eared bats in urban and suburban landscapes prior to WNS largely are unknown. Northern long-eared bat maternity colony research prior to the advent of WNS observed >80 bats in roosts (Owen et al., 2002). However, we do not know if this particular colony at the Estate existed prior to WNS and if it did, either its membership number or spatial extent.

Despite being a small colony, bats in our study used a similar number of roosts throughout their tracking periods as with other studies (between 2.2 and 3.6 roosts per bat, with a maximum of 5 or 6; Foster and Kurta, 1999; Hyzy et al., 2020; Sasse and Pekins, 1996; Silvis et al., 2014a), suggesting that they are maintaining similar roost-switching patterns to pre-WNS and in other landscape and habitat types. Our bats, and others, tended to switch roosts between every 1–2 days with little variation (Foster and Kurta, 1999; Garroway and Broders, 2007; Hyzy et al., 2020; Patriquin et al., 2010; Silvis et al., 2014a). Further, the distance our bats travelled between subsequent roosts also was fairly consistent with the findings of others (333 m \pm SD 88 m and 227 m \pm SD 161 m; Foster and Kurta, 1999; Henderson and Broders, 2008, respectively), despite our study area being a spatially-constrained forest patch in the middle of suburbia. Similar to Henderson and Broders (2008), when bats were tracked to roosts outside of forested areas, we observed all were <80 m from the forest edge – well below their recorded average nightly movement between roosts. The middle of the Estate is comprised of grassy meadow that quickly transitions to a woody marsh in the southern portion of the property (bordering the ocean), which would likewise be considered poor habitat for northern long-eared bats. This leads us to question whether or not this colony is being forced into a concentrated forest patch due to lack of suitable, surrounding habitat.

While we do not know for sure that these colony members were staying within the Estate, we have no evidence to suggest that they would be traversing >3 km through suburbia to the nearest forest patches.

Our utilization distribution showed this colony made greater use of the forested edges of the Estate than the central forested portions of the Estate, demonstrating the importance of heterogeneous habitat (Carter and Feldhamer, 2005; Gorman et al., 2022b; Pauli et al., 2015), perhaps because in such a small area there were more suitable roost options along the edges of the property, i.e., snags, poor form trees with cavities and higher solar exposure. This is contrary to Thorne et al.'s (2021) findings for an urban colony of northern long-eared bats in Toronto, Ontario, Canada, which exclusively used interior forest and natural roosts. The locations of the primary roosts at the extreme north and west edges of the Estate boundaries (bordering the neighborhood) may point to an adaptability to human-disturbed landscapes rarely noted for this species in the past. Ford et al. (2016), Johnson et al. (2012), and Silvis et al. (2014a) all demonstrated the flexibility of northern long-eared bat social networks to adapt to changing forest habitats from disturbance such as fire or forest harvesting that changed roost availability and roost conditions. Unlike our study, these efforts occurred in very large forested landscapes with a great range in forest condition and a high number of potential day-roosts adjacent to disturbed patches.

Due to the small forest patch size of the Estate, our high mean degree values showed little distance between individual bats and roosts in this network. In other words, roosts that were not primary nodes were still being used by multiple bats, and there were frequent returns to communal roosts. Invariably, our finding could be skewed by short tracking periods and the high number of captures at a primary roost. The higher degree centralization index for the roost network shows that the primary nodes (the bat house and one of the utility poles) were integral to driving the connectivity of the network. The degree centralization indices for bats within the network have varied by colony in other studies (range 0.19–0.99; Hyzy et al., 2020; Silvis et al., 2014a). Our results fall on the low end, indicating that all of our bats were equally connected to one another and no specific individuals were driving the connectivity of the network. The high betweenness ranking for the bat network reveals that bats had many connections *through* other bats, whereas the low betweenness ranking for the roost network means roosts were often *directly* connected to one another through few bats rather than being *indirectly* connected (e.g., hypothetical roosts A, B, and C are all connected to one another through single bats, rather than nodes A and C being connected *through* bats that also roost in B). We speculate that the juvenile male and adult female that were not connected to the larger network were likely part of the same colony considering the small and isolated area of the Estate. As such, if given longer tracking times (or earlier capture), we believe these two bats would have been connected to the larger group. Ultimately, these two bats were left

out of the network analysis because we had no definitive proof of their inclusion in the colony, though we doubt there was another maternity colony on or near the Estate.

The low clustering value, in comparison to other studies (range 0.57–0.86; Garroway and Broders, 2007; Patriquin et al., 2010; Silvis et al., 2014a), reinforces the low degree centralization and high betweenness results, as it demonstrates a lack of preferential groups within the context of the whole study. In short, many individual bats are connected to many other individual bats through a larger number of shared roosts, rather than *only* being connected through the utility pole and bat house roosts that we considered primary roosts. Our bat network density was higher than typically reported in other studies (range 0.11–0.67; Hyzy et al., 2020; Silvis et al., 2014a), and our roost network density was in the range of other findings. Although our short tracking periods could be contributory to this finding, it more likely reflects the concentration of comparatively better habitat of the Estate versus the surrounding suburban areas (Ford et al., 2016; Hyzy et al., 2020).

Taken together, all of the network structural measurements we calculated point to a highly-organized social network in which connections between bats and roosts are evenly distributed. The small forest patch size of this study may be functioning to elucidate patterns of connectivity between bats that is more difficult to ascertain in areas with more resources. Although some bats may have closer relationships with one another, or cliques, as indicated by roosting patterns, they still remain highly social with the entire colony. This mirrors the two-level society concept provided by Garroway and Broders (2007), whereby bats are categorized as “constant companions” or “casual acquaintances”. Given a longer tracking period throughout the maternity season, we might have seen these measurements change to reflect weaker relationships between cliques (the “casual acquaintances” dissipating whereas the “constant companions” remain as close associates) as colony disassociation begins at the end of the maternity season (Garroway and Broders, 2007; Hyzy et al., 2020; Johnson et al., 2012). Disease and parasite transmission potentially would be higher in this type of network because of the tendency for large numbers of bats to congregate in the same place on the same days (Ford et al., 2016; Johnson et al., 2012; Kerth, 2008a).

More important than any individual bat, the primary roosts (the bat house and one of the utility poles) were the critical loci of this colony during the period we tracked bats. Aside from meeting thermoregulatory needs during pregnancy, this could indicate that social rearing of offspring is especially valuable to this colony (Johnson et al., 2012; Kerth, 2008a), even outside the most-energetically costly period of lactation (Garroway and Broders, 2007). However, as both of the primary nodes within the network were humanmade structures (not trees or snags), we believe this could be an indication that the

Estate really only provides a more suitable foraging habitat for the colony and that roosting needs are not being sufficiently met by the current forest condition. With no known colonies nearby and several shared roosts, it is possible that a stochastic or intentional removal event of secondary roosts would not necessarily be overly deleterious if primary roosts remained (Rhodes et al., 2006). However, primary roost loss due to stochastic weather events or human intervention could be disruptive to the entire social structure of this colony. For a big brown bat (*Eptesicus fuscus*) maternity colony, Brigham (1991) found that reproductive success was negatively impacted when the bats lost access to a primary roost. In a small colony such as the one we tracked, reproductive failure could lead to a swift colony collapse as new colony members are generally the offspring of current members (Olivera-Hyde et al., 2019). In this case, in this particular setting, installation of additional artificial roost structures or forest management that would add additional roosts or improve current roost conditions could be a warranted conservation action (De La Cruz et al., 2018; Johnson et al., 2010; Schroder and Ward, 2022). As climate change continues, the risk of extreme weather events such as hurricanes are a threat that is unique to these coastal environments and which upland, inland forests traditionally associated with northern long-eared bats do not face. Additionally, as humans move to more urban areas, and the demand for land goes up, it will become more imperative that imperiled wildlife is not pushed out or forced to come into contact with humans. In the case of northern long-eared bats, this could mean that an increased use of inhabited structures such as attics or cellars, and forced ejection from the units.

Our work demonstrates that even small patches of forest in areas surrounded by high human development can support reproductively-successful maternity colonies of northern long-eared bats in the post-WNS environment. Similar to other studies, bats in this colony often broke off with one or two other bats that were presumably preferred over other colony members, but at the Estate no individual or subgroups of bats were necessarily driving the connectivity of the network as a whole more than others. Rather, the roosts as communal meeting areas or shared spaces were integral to the cohesion of the colony. In that case, the survival of this colony, and presumably others in similar urbanized settings (Deeley et al., 2021) could be precarious due to less alternative roost availability. There is evidence that focal points of similar networks of Indiana bats (*Myotis sodalis*) may shift across the landscape over time (Kurta et al., 2002) or in response to roost loss (Silvis et al., 2014b); such a shift would not be possible for the bats of this colony unless they left the Estate entirely. Although these bats may be showing an increased tolerance for fragmented or human-disturbed habitat, there may be an upper limit to how far the colony would move as a unit to reach other areas with sufficient roost options. And because northern long-eared bats, over decadal periods, do rely on a shifting mosaic of suitable forest conditions (Silvis et al., 2012), smaller, isolated forest patches may not contain suitable day-roost conditions at various

intervals along the forest succession and stand dynamics process (Oliver and Larson, 1996). Accordingly, perpetuation of day-roost habitat in urbanized landscapes may require more management intervention such as placement of artificial roost structures or snag creation than in large forested landscapes to retain local northern long-eared bat viability.

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Tables

Table 0-1. Number of days tracked (across both years), number of roosts used, and minimum, mean, and maximum distance (m) travelled between subsequent roosts for northern long-eared bats (*Myotis septentrionalis*) at the William Floyd Estate, New York (2018–2019).

Bat	Tracking days	Number of roosts	Minimum distance (m)	Mean distance (m)	Maximum distance (m)
72400	3	2	212.9	212.9	212.9
72401	3	3	98.04	420.09	742.95
72402	7	3	0	120.5	550.6
72403	1	1	0	0	0
72405	4	2	0	276.5	829.5
72406	8	6	0	318.29	829.48
72407	7	5	0	384.48	1233.09
72408	6	4	0	265.29	829.48
72409	5	3	0	345.4	829.5
72410	2	1	0	0	0
72411	14	6	0	128.3	829.5
72412	1	1	0	0	0
72413	5	4	0	272.52	650.08
72414*	4	2	0	221	663
72418*	4	3	0	43.89	81.06
RRR034	5	4	0	192.5	299.7

* Bats 72414 and 72418 were presumably part of the colony but we did not have direct evidence of this connection for this study. As a result, they were not included in the network analysis.

Figures



Figure 0-1. Nursery box used by northern long-eared bat (*Myotis septentrionalis*) maternity colony just outside the William Floyd Estate, New York (2018).



Figure 0-2. Utility pole used by northern long-eared bat (*Myotis septentrionalis*) maternity colony just outside the William Floyd Estate, New York (2018–2019).

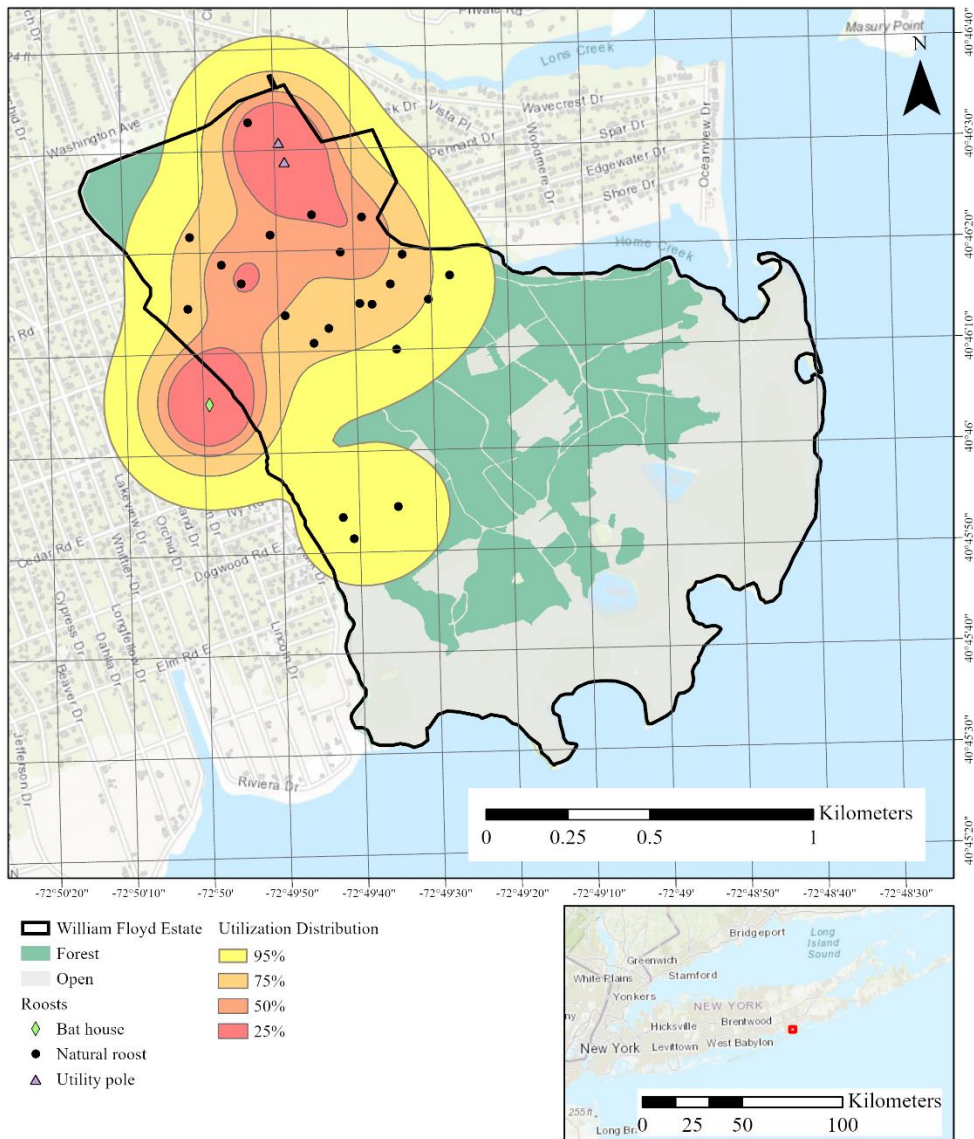


Figure 0-3. Utilization distribution for northern long-eared bat (*Myotis septentrionalis*) maternity colony at the William Floyd Estate, New York (2018–2019). Contour lines show 25%, 50%, 75%, and 95% utilization distributions. Utility poles and the bat house are shown as purple triangles and a green diamond, respectively. Natural (tree) roosts are shown as black points. Map created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Copyright © Esri. All rights reserved. For more information about Esri® software, please visit www.esri.com.

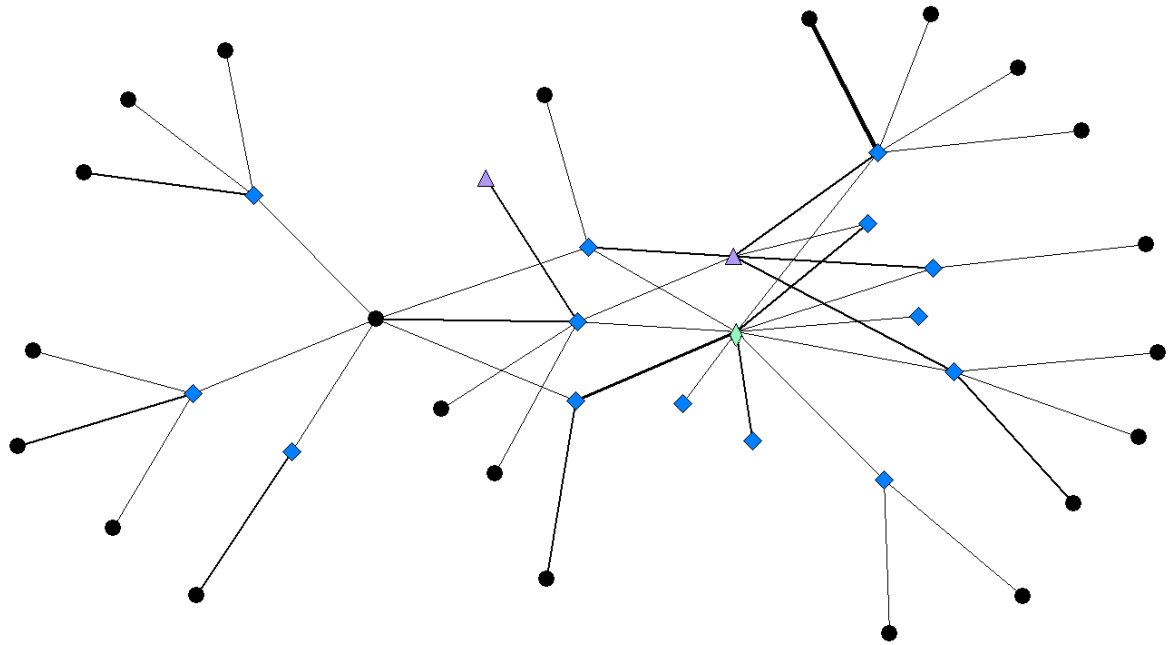


Figure 0-4. Scale-free bipartite network visualization for northern long-eared bat (*Myotis septentrionalis*) maternity colony at the William Floyd Estate, New York (2018–2019). Green diamond node represents the bat house, purple triangle nodes represent utility poles, black circle nodes are natural roosts (tree or snag), and blue diamonds are bats. Line weights represent the strength of the connection.

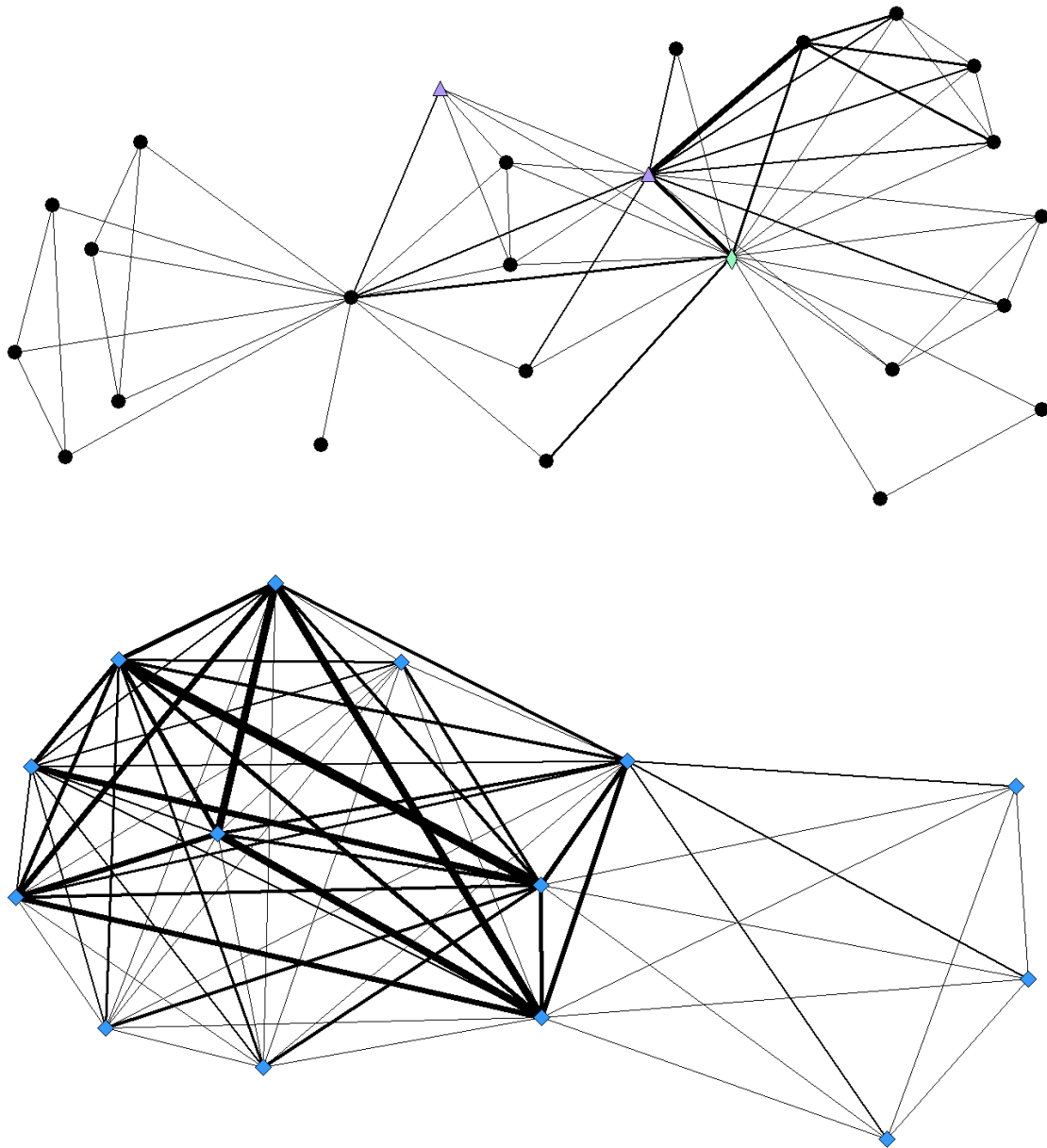


Figure 0-5. [Top] Roost network visualization for northern long-eared bat (*Myotis septentrionalis*) maternity colony at the William Floyd Estate, New York (2018–2019). The green diamond node represents the bat house and the purple triangle nodes represent utility poles. One utility pole was used by bats both years. [Bottom] Bat social network visualization for northern long-eared bat maternity colony.

Overall conclusions

As in-hand confirmations and acoustic detections of northern long-eared bats (*Myotis septentrionalis*) are decreasing throughout North America due to a declining population and local extirpation, effective management strategies and conservation measures that are species-specific are needed. Interpretation of acoustic detections will be increasingly more critical in monitoring and assessment efforts as this species becomes even more rare, and will aid in delineating potential conservation units and performing management actions therein. Rather than adopting management protocols from other bat species that have distinct and differing ecological needs than northern long-eared bats, species-specific guidelines are needed to address conservation measures in areas that have known populations of northern long-eared bats.

The importance of riparian areas and water features in predicting higher levels of northern long-eared bat acoustic activity – particularly in those areas with confirmed female presence in the summer indicative of potential reproduction – was initially underscored in the results of 0. This positive relationship was further supported in 0, with distance from day-roosts to water features having one of the best statistical predictors of use. As the proposed rule to list northern long-eared bats as Endangered progresses, the significance of riparian areas to their nightly foraging and commuting activities should explicitly be included in U.S. Fish and Wildlife Service monitoring protocols and management guidelines.

Additionally, maintaining and promoting heterogeneity in forest structure, age class and composition to provide suitable foraging and day-roosting habitat should be a management priority. At the broad scale, forest cover is critical in supporting northern long-eared bat populations. However, at the fine (detector-level) scale within forests themselves, forest edge and access to commuting corridors will support higher levels of acoustic activity that are presumably indicative of better foraging habitat (0) and day-roost options (0), even in areas with less forest coverage overall (0). My dissertation highlights the importance of even small forest patches in highly developed, coastal areas to the reproductive success of persisting northern long-eared bat maternity colonies. As a species that has previously been considered a strict upland forest obligate, this finding will be critical to management considerations going forward and may require a reassessment of managers' conventional notion of suitable northern long-eared bat areas.

Artificial day-roosting structures such as bat boxes are heavily used resources for small colonies of northern long-eared bats in areas with fragmented forest coverage, as they provide reliable day-roosts

across years that would be less susceptible to detrimental stochastic events, such as extreme weather (0) or natural stand dynamic and successional processes (0). 0 also emphasizes the high use and importance of these semi-permanent structures to maintaining bat colony cohesion and reinforcing colonial success. As increasing numbers of successful, albeit small, maternity colonies of northern long-eared bats are observed along the Atlantic Coast, researchers and managers need to become aware of the most effective conservation strategies for this species. Whether these coastal populations are summer residents, migrants passing through, or even overwintering, the changing climate and potential increase in hurricane activity and intensity may negatively impact the integrity of current available foraging habitat, day-roosts, and social connections that support this species in coastal environments (0, 0, 0).

Future research on the use of anthropogenic structures in developed, coastal areas should be conducted. The installation of bat boxes according to the criteria outlined in 0, in areas with active maternity colonies, could be useful in monitoring the long-term reproductive success of these colonies as well as determining whether this increased tolerance for human-developed landscapes are colony-specific or more widespread. Radio-tagging and tracking of northern long-eared bats in the fall, or the use of other tracking technologies such as the Motus Wildlife Tracking System, could help determine whether northern long-eared bats are overwintering locally on Long Island or migrating to traditional hibernacula later in the year.

Despite northern long-eared bats being somewhat tolerant to anthropogenic development and diverse types of habitats, managers need to have a greater understanding of the most effective measures to support remaining populations in order to discourage genetic bottlenecks and local extirpation to range-wide extinction events. This dissertation provides some (general and specific) habitat features that should be considered when crafting species-specific conservation measures for northern long-eared bats – particularly in more urban, isolated forest patches in coastal areas.

In the updated 3-Bat Species Status Assessment of 2022 (SSA; U.S. Fish and Wildlife Service, 2022), water resources are broadly mentioned as an important ecological requisite for northern long-eared bats. More specific language should be included about the size, condition and type of water features within the forest landscape. Additionally, while forest condition heterogeneity is stressed relative to landscape or resiliency to changing climate, few specifics to inform management of the species were provided. Lastly, in light of my findings in 0 and 0, the SSA undermines the importance of including artificial structures in smaller forest tracts in coastal areas that are potentially more susceptible to stochastic roost-loss events.

Literature cited

U.S. Fish and Wildlife Service, 2022. Species Status Assessment Report for the Northern Long-eared Bat (*Myotis septentrionalis*; U.S. Fish and Wildlife Service Version 1.1). Bloomington, Minnesota.