



Broad-scale geographic and temporal assessment of northern long-eared bat (*Myotis septentrionalis*) maternity colony–landscape association

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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 is 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 is the most effective strategy for identifying potential active northern long-eared bat maternity colonies on the local landscape.

KEY WORDS: Acoustic surveys · Bat activity · Coastal environment · Maternity colony · *Myotis septentrionalis* · Riparian · Northern long-eared bat

1. 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, Threlfall et al. 2012, Rodríguez-San Pedro & Simonetti 2015). 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 & 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

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listed as Threatened under the Endangered Species Act (ESA) since 2015 (US Fish and Wildlife Service [USFWS] 2015). It currently is undergoing an additional assessment for possible up-listing to Endangered in the United States (Bies 2020, J. Jaka USFWS pers. comm.). 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 (Silvis et al. 2016, Hyzy et al. 2020a). 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 (Francl et al. 2012, Barr et al. 2021). 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 & O'Dell 2018, Jordan 2020), as well as a few residual populations in interior regions similarly distant (De La Cruz 2021).

Understanding activity patterns related to reproductive periods is necessary for developing monitoring approaches. After parturition, juveniles remain non-volant for about 3 wk (Krochmal & 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 (elevation 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 (Jordan 2020, Gorman et al. 2021) 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 (USFWS 2020a) 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 (USFWS 2015, Ford et al. 2016). 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 (USFWS 2020b). 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 (Owen et al. 2003, Garroway & Broders 2008, 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 & 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.

2. MATERIALS AND METHODS

2.1. Sampling regions

Our study area included 7 mid-Atlantic sampling regions where we documented reproductive female or juvenile northern long-eared bats (Fig. 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 3 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 pseudoacacia*, 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 3 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).

2.2. 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 (Silvis et al. 2012, Deeley 2019). Demographic data were recorded for all bats captured, which included species, sex, and age class (adult or juvenile; Brunet-Rossini & 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-

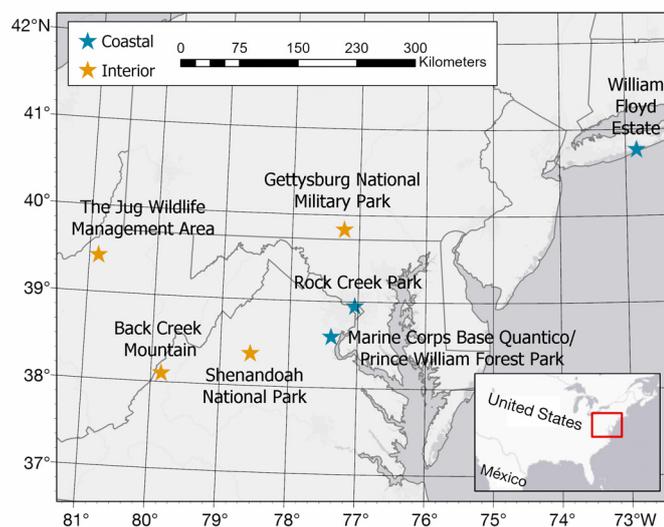


Fig. 1. Coastal and interior northern long-eared bat (*Myotis septentrionalis*) sampling regions, 2015–2020

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 (Ford et al. 2005, Austin et al. 2018, 2020, Barr et al. 2021, Deeley et al. 2021). At most sampling regions, acoustic recording occurred the same year(s) as mist-netting efforts (see Table 1 for details). 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 to 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.

2.3. 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 dis-

solved 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 (Figs. 2 & 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

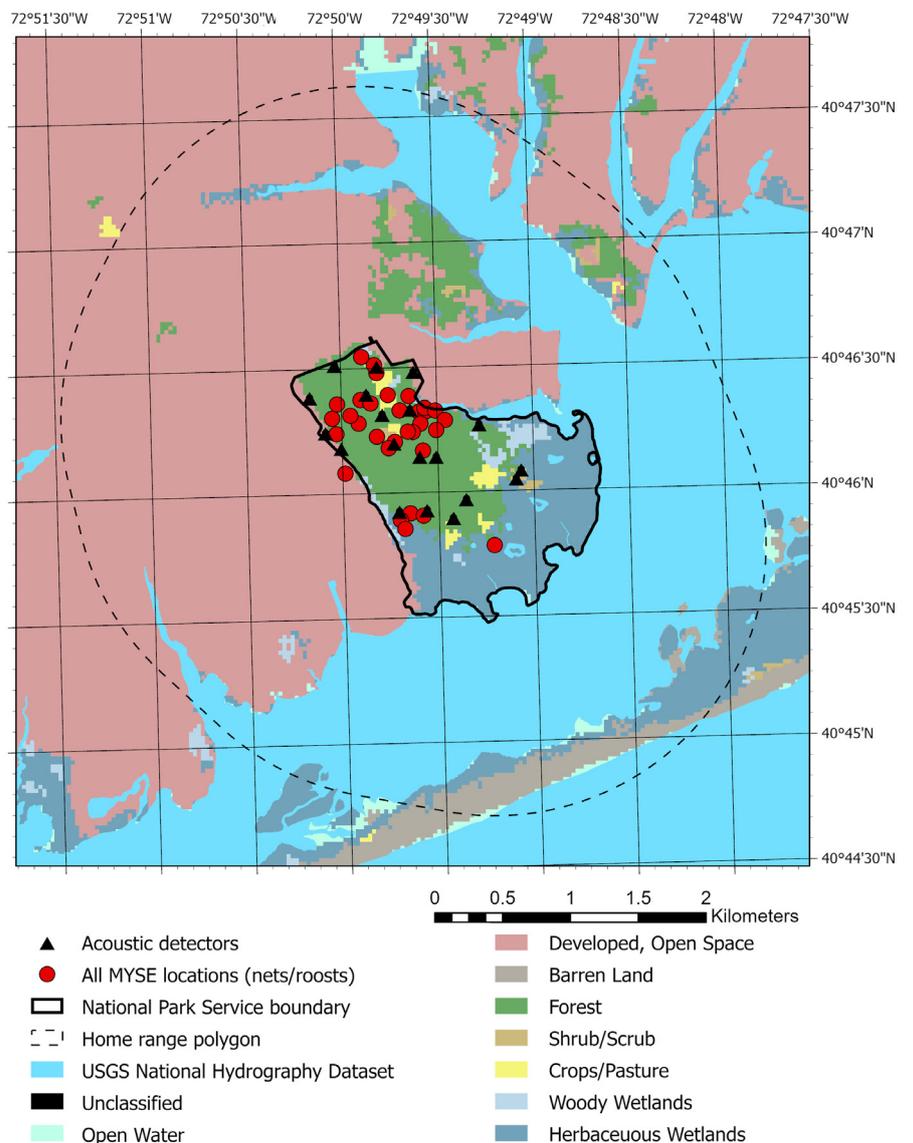


Fig. 2. Example of a coastal sampling region showing capture and day-roost sites of northern long-eared bats *Myotis septentrionalis* (MYSE) and acoustic sites used in analysis on William Floyd Estate, Fire Island National Seashore, New York (2018–2020). Map shows broad land cover category and estimated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

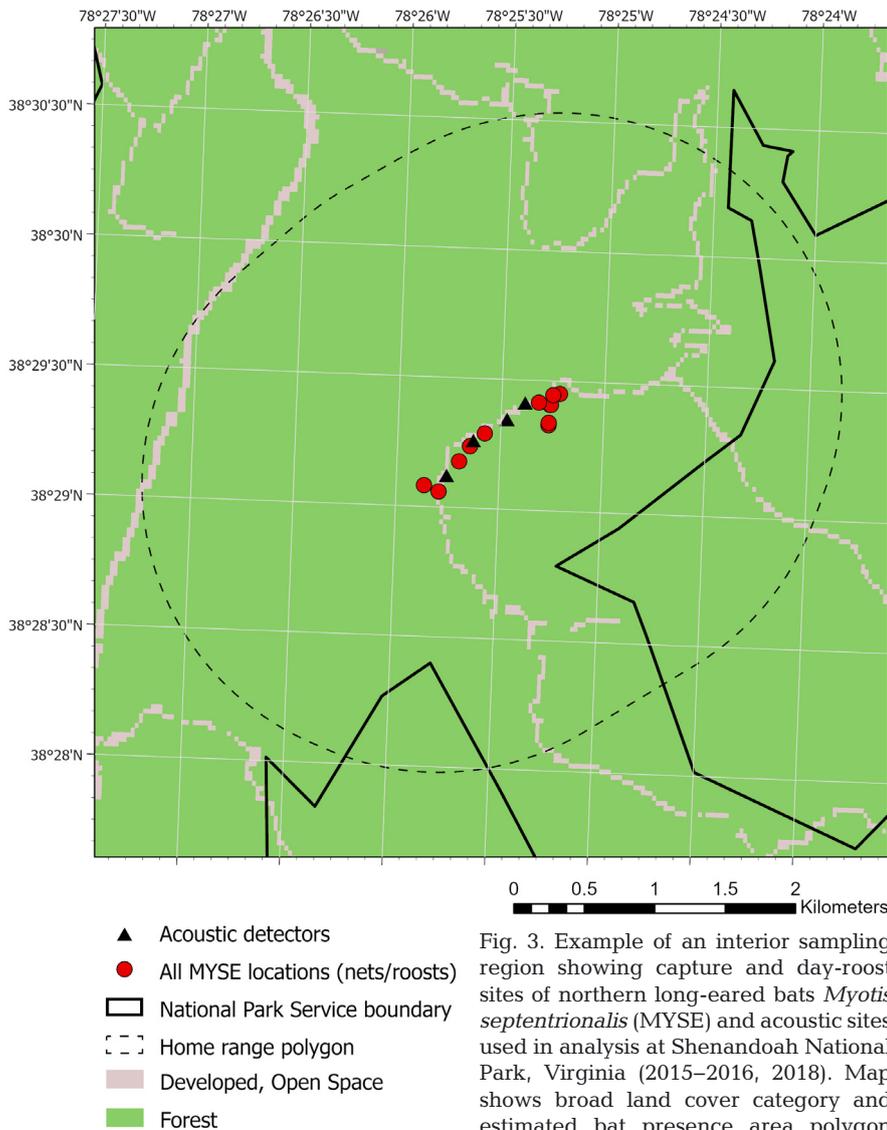


Fig. 3. Example of an interior sampling region showing capture and day-roost sites of northern long-eared bats *Myotis septentrionalis* (MYSE) and acoustic sites used in analysis at Shenandoah National Park, Virginia (2015–2016, 2018). Map shows broad land cover category and estimated bat presence area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

required for documenting northern long-eared bat presence (USFWS 2020b). However, we set a minimum threshold of 3 pulses per call file (as opposed to the 2 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 (USFWS 2020b), we only included nights without precipitation using weather data from Aviation Routine Weather Reports (Iowa Environmental Mesonet 2020). We combined 3 National Land Cover Dataset (NLCD; Multi-Resolution Land Characteristics [MRLC] Con-

sortium 2016) forest land cover types: deciduous forest, evergreen forest, and mixed forest into 1 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 (USGS 2020) or NLCD wetland/open water (MRLC 2016), 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.

2.4. 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; our Fig. A1 in the Appendix) 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 sam-

pling 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 (Rydell 1993, Ford et al. 2011, Deeley et al. 2021). Using this information, we approximated a general juvenile volancy start date at the low point between the 2 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 & Simko 2017) and found no correlation ≥ 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 2 to 5 covariates based on our ecological understanding of northern long-eared bats and their use of riparian habitat (Owen et al. 2003, Ford et al. 2005, 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 & Anderson 2002) and considered all models within $\Delta AIC < 2$ to be potentially informative (Burnham & 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).

3. RESULTS

At our coastal sampling regions, we delineated presence area polygons ranging from 2133 to 5750 ha (Table 1). At our interior sampling regions, we delineated presence polygons ranging from 1911 to 3319 ha (Table 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 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.

Table 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	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 Area, 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
Prince William Forest Park/ Marine Corps Base-Quantico, Virginia	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	0.168 \pm 6.35
William Floyd Estate, New York	Coastal	26	2018–2019	2018–2020	2133	19	2997	4.19 \pm 56.21

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

Northern long-eared bat acoustic activity was higher throughout the pre-volancy period ($p < 0.001$; Table 3, Fig. 4). 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 ($p < 0.001$; Fig. 5). 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, $p < 0.001$; Fig. 6). Acoustic activity increased with increasing distance from known roost or capture site ($p < 0.001$; Fig. 7).

Table 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 acoustic site forest: 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
Acoustic site forest	-3.46	0.77	-4.48	<0.001	-4.98	-1.95

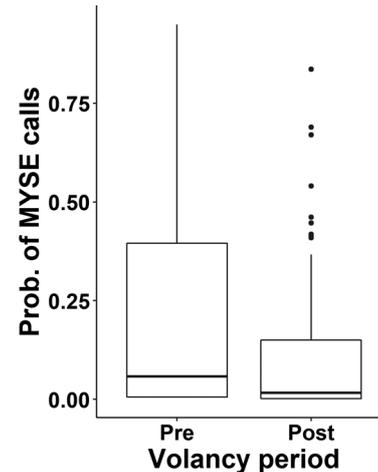


Fig. 4. Predicted pre- (before June 24) and post-volancy (June 24 and later) probability (Prob.) of activity for northern long-eared bats *Myotis septentrionalis* (MYSE), 2015–2020. Boxes represent 50% of the data, horizontal line in the box represents the median, whiskers represent the extent of roughly 97% of the data, and dots represent outliers

4. 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 tra-

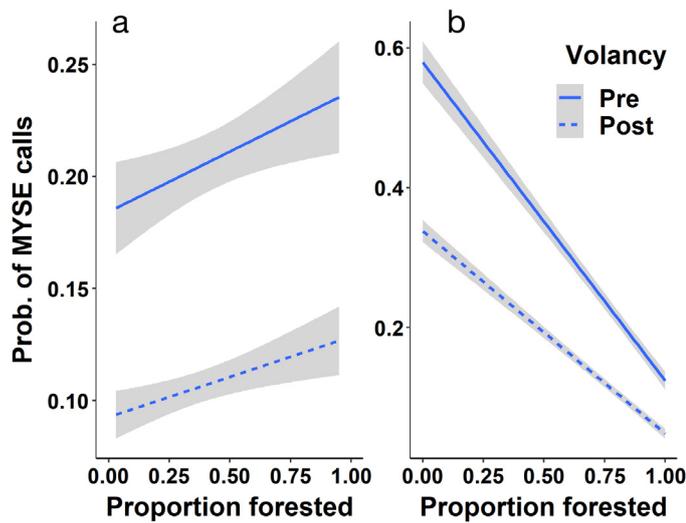


Fig. 5. Predicted effects of percent forest cover (a) within the presence area polygon and (b) within 30 m of acoustic sites on predicted probability (Prob.) of northern long-eared bat (*Myotis septentrionalis* [MYSE]) nightly calls, 2015–2020. Note the different y-axis scales. Shaded areas: 95% CIs; dashed lines: pre-volancy period (before June 24); solid lines: post-volancy period (June 24 and later)

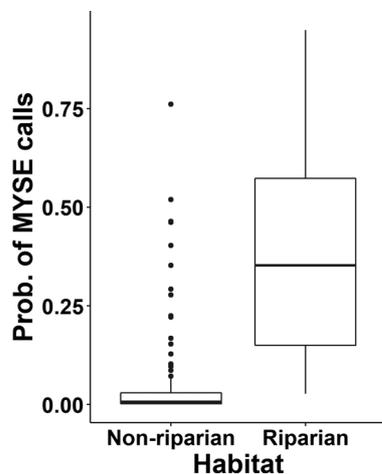


Fig. 6. Predicted effects of riparian habitat on probability of activity for northern long-eared bats *Myotis septentrionalis* (MYSE), 2015–2020. Boxes represent 50% of the data, horizontal line in the box represents the median, whiskers represent the extent of roughly 97% of the data, and dots represent outliers

ditional 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 & O'Dell 2018).

The USFWS considers the northern long-eared bat a forest-dwelling and clutter-adapted foraging spe-

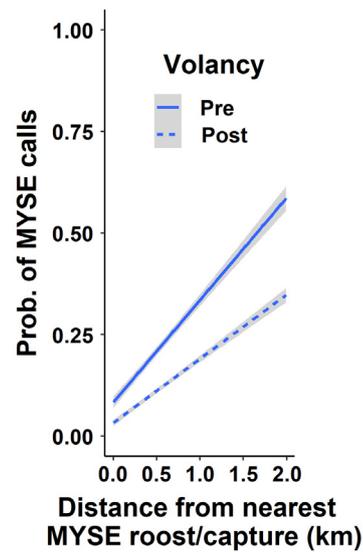


Fig. 7. Predicted effects of distance from nearest northern long-eared bat (*Myotis septentrionalis* [MYSE]) capture site or roost on predicted probability of nightly activity, 2015–2020. Shaded areas: 95% CIs; dashed lines: pre-volancy period (before June 24); solid lines: post-volancy period (June 24 and later)

cialist species (Carter & Feldhamer 2005, USFWS 2015, Silvis et al. 2016), largely emphasizing the importance of forest retention as a conservation strategy (Russo & 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 & 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, Thalken et al. 2018, Hyzy et al. 2020b). 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 (Vaughan et al. 1997, Russo & Jones 2003, Ober & Hayes 2008). 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; Vaughan et al. 1997, Russo & Jones 2003), 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 2 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.

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Appendix.

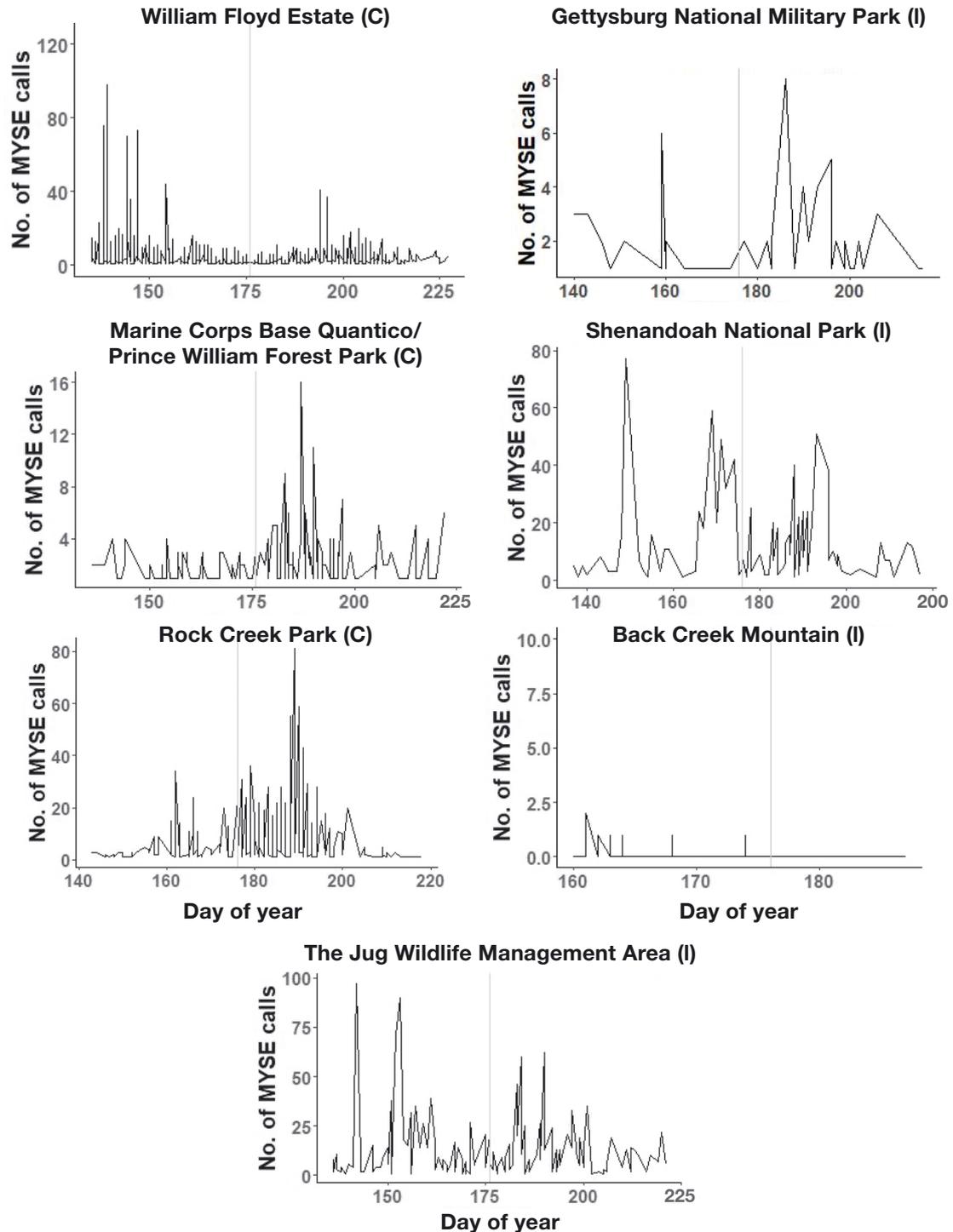


Fig. A1. Total northern long-eared bat (*Myotis septentrionalis* [MYSE]) nightly calls during analysis period (May 15–August 15) at coastal (C) and interior (I) sampling regions. William Floyd Estate y-axis adjusted for visibility, cutting off 7 points before day of year 150. No. of MYSE calls: total number of northern long-eared bat call files per night; vertical gray lines: distinction between pre- and post-volancy dates. See Table 1 for timeframes of data used at each survey site