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Article in *Endangered Species Research* · June 2024

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Widespread occupancy of the endangered northern myotis on northeastern Atlantic Coastal Plain islands

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ABSTRACT: Northern myotis *Myotis septentrionalis* are one of the bat species most affected by white-nose syndrome (WNS), and disease-induced declines may cause compounding effects when combined with other threats such as habitat loss and fragmentation. Recent evidence suggests that peripheral populations are persisting in post-WNS years; however, the environmental factors that influence the occurrence of this species along the Atlantic Coastal Plain are virtually unknown. We conducted a large-scale acoustic survey on 3 islands: Long Island, New York, and Martha's Vineyard and Nantucket, Massachusetts, USA, and used a multi-scale occupancy modeling approach to determine the landscape and abiotic factors affecting the distribution of northern myotis. Our estimates of occupancy and detection probability suggest widespread presence across the islands. At the local (200 m) scale, we identified strong negative effects of development on Long Island and Nantucket and a strong positive effect of forest habitat on Martha's Vineyard. None of the variables we measured sufficiently explained the landscape (1 km²) occupancy of this species, which was very high ($\psi = 0.81–0.97$), representing an outlier for this species in the post-WNS landscape. The lack of association at the landscape scale suggests that general differences in land cover are not a driving factor of higher occupancy of peripheral northern myotis populations, while local site-specific conditions may be supporting critical foraging or roosting habitat. Because islands are particularly vulnerable to human-driven habitat alteration due to the constraint of limited space, and development pressure is expected to increase, this study provides a baseline to enable managers to assess the effects of future environmental disturbances and monitor population trends to support long-term survival of northern myotis.

KEY WORDS: Northern myotis · Coastal distribution · Peripheral populations · White-nose syndrome · Multi-scale occupancy modeling

1. INTRODUCTION

Temperate bat species are facing threats from multiple anthropogenic stressors, including habitat loss

or degradation (Fenton 1997, Frick et al. 2020), the introduction of pathogens (Drees et al. 2017), and wind energy development (Arnett & Baerwald 2013), which may act synergistically to impose cumula-

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tive impacts on populations. White-nose syndrome (WNS) is a recently emerged infectious disease in North America, caused by the fungal pathogen *Pseudogymnoascus destructans* (Blehert et al. 2009). Since its introduction to New York in 2006, the disease has been responsible for large mortality events and continues to pose a substantial threat to many hibernating bats as it spreads across the continent (Frick et al. 2015, Hoyt et al. 2021). WNS does not affect all species equally, and while some populations continue to decline or become locally extirpated (Langwig et al. 2012, Frick et al. 2015), others have stabilized at reduced population densities or are currently increasing following initial declines (Langwig et al. 2017, Hoyt et al. 2021). Understanding the environmental factors that support persisting populations has become fundamental to inform management efforts aimed at protecting these species of conservation concern.

Formerly one of the most common bats throughout eastern North America, the northern myotis *Myotis septentrionalis* has since declined >90% throughout most of its range due to its high susceptibility to WNS (Cheng et al. 2021). This species was one of the first bats listed under both the US Endangered Species Act and the Canadian Species at Risk Act (endangered, COSEWIC 2012; threatened, US Fish and Wildlife Service [USFWS] 2015) as a result of WNS-associated mortality and subsequent population declines. Recent studies have documented a reduction in both range and activity for this species in the northeastern USA, and estimates show that it currently occupies only a portion of its former range within the region (35%) in post-WNS years (De La Cruz et al. 2019). Given the predicted high risk of extinction and continued declines in abundance and occurrence range-wide (Frick et al. 2017), northern myotis were recently reclassified to endangered status in the USA, as WNS remains the most severe and pervasive threat for this species (USFWS 2022).

Primarily described as a forest-dwelling and clutter-adapted species, previous studies of northern myotis have predominantly focused on large, forested landscapes (Menzel et al. 2002, Owen et al. 2003, Lacki et al. 2009) and the response to forest management practices (Johnson et al. 2012, Ford et al. 2016, Alston et al. 2019). Despite adaptations for forested environments, anthropogenic roost use appears more common than previously thought (Hoff et al. 2024), and several observations of this species in post-WNS years have occurred in developed landscapes (Dowling & O'Dell 2018, Deeley 2019, Thorne et al. 2021, Gorman et al. 2022a).

Additionally, recent evidence suggests peripheral populations of northern myotis along the Atlantic Coastal Plain are persisting in post-WNS years (Grider 2016, White et al. 2018, De La Cruz et al. 2020, Jordan 2020, Hoff et al. 2024), although the current population trend is unknown. This region is considered a global biodiversity hotspot, characterized by a high degree of unique habitat types and threats of extensive habitat loss (Noss et al. 2014). Northern myotis have been documented in large, forested tracts that remain in portions of the region (Grider et al. 2021), in addition to intensively managed forests (Jordan 2020), yet they are also found in areas experiencing fragmentation due to intense development pressure (Rogan et al. 2016, Gorman et al. 2022a), particularly on northeast coastal islands where land area is limited. Northern myotis presence and habitat preference has been largely understudied within this region; however, understanding the ecology of this now rare species persisting at the edge of its range is exceedingly important to support conservation efforts.

As WNS continues to spread and bat populations are reduced, traditional monitoring protocols relying on capture are becoming largely ineffective due to the high level of effort needed to detect declining species (Coleman et al. 2014). Managers are turning to non-invasive sampling techniques such as acoustic monitoring to document presence and quantify activity of bats in the environment (Deeley et al. 2021, USFWS 2023a). A common approach to monitoring the population status of rare species is occupancy estimation, which relates predictor variables to occurrence records while explicitly accounting for imperfect and variable detection probabilities (MacKenzie et al. 2002). Bat distributions may be influenced by a variety of factors at both the landscape and local scale that support foraging and roosting behavior, including the configuration of habitats, presence of suitable roosting structures, frequency and level of disturbance, proximity of forested riparian habitats, and availability of invertebrate prey (Ober & Hayes 2008, Silvis et al. 2014, Pauli et al. 2015), so utilizing a multi-scale occupancy framework will allow us to evaluate ecologically relevant hypotheses related to hierarchical habitat use (Green et al. 2019).

Understanding the distribution of a rare species is a first step in supporting its conservation, and improving the knowledge of the habitat associations of northern myotis populations occurring along the edge of their range will aid in the development of effective management plans. We sought to better understand the occupancy and environmental associa-

tions of persisting peripheral populations at multiple spatial scales. The specific objectives of our study were to (1) investigate the distribution and environmental associations of northern myotis across 3 coastal islands, with a focus on human development, and (2) assess factors that influence detection probability to determine the appropriate level of intensity of sampling effort needed to effectively monitor these populations. We predicted that northern myotis would be positively associated with forest cover and large forested patches (relative to the mean patch area of our study sites; 542 acres [219 ha]), given their affinity for contiguous forest (Owen et al. 2003, Henderson & Broders 2008) and high canopy cover (Lacki & Schwierjohann 2001, Menzel et al. 2002), but that we would not detect a strong negative relationship to surrounding development, based on previous observations of anthropogenic roost use (Hoff et al. 2024).

2. MATERIALS AND METHODS

2.1. Study area

We conducted our research on 3 islands along the coastal northeastern USA: Long Island, New York; and Martha's Vineyard and Nantucket, Massachusetts. Our study area on Long Island targeted Suffolk County (approximately 2362 km²), covering the central and eastern portion of the island, and excluded the counties further west (Brooklyn, Queens, and Nassau) due to high human population density. The north shore of Suffolk County is 6–20 km away from the mainland, and >50% of the land cover within the county comprises developed open space and low- to medium-intensity development (National Land Cover Dataset [NLCD] categories, Dewitz & USGS 2019; our Table 1). Prominent habitat types include fire-adapted shrublands and grasslands, pine barrens, coastal plain ponds, and

deciduous forest. Martha's Vineyard (227 km²) is located approximately 11 km from mainland Massachusetts across the Vineyard Sound and has a year-round human population of 17 265 that triples with tourism during the summer months. Nearly 40% of the island is protected natural space, with much of the development concentrated in 3 towns on the eastern coast. The northern portion of the island is terminal moraine dominated by mesic forest with many kettle ponds, while the central and southern portion of the island consists of outwash plain with a variety of habitats, including mixed oak and pitch pine forests, pine and scrub oak barrens, coastal heathlands, and sandplain grasslands (Swain 2020). Nantucket (124 km²) is a remote island community located 48 km from mainland Massachusetts with a year-round human population of 11 327 that in summer increases to >50 000. About 50% of the island is protected land comprising sandplain grasslands, sandplain heathlands, scrub oak and pitch pine barrens, and maritime shrublands, with small pockets of hardwood forests interspersed throughout. The first WNS detections on the islands were in 2011, 2017, and 2020 on Long Island, Martha's Vineyard, and Nantucket, respectively.

2.2. Sampling site selection

Using digital mapping software (ArcMap v.10.7.1, ESRI), we generated a grid system of 1 km² units across each island. We used the 2016 NLCD tree canopy cover spatial dataset to classify each grid cell by average canopy coverage (Dewitz & USGS 2019). We selected sample units using a stratified random sampling scheme from 5 categories based on percent canopy cover (0–20, 21–40, 41–60, 61–80, 81–100%). Due to the large differences in area among the islands, 50 units were selected for

Table 1. Land cover and land use characteristics for Suffolk County, Long Island, Martha's Vineyard, and Nantucket. Land cover measures: % of total island area. Data from the 2016 National Land Cover Dataset (Dewitz & USGS 2019) for Long Island and the 2016 C-CAP Land Cover Massachusetts Land Cover/Land Use Dataset (OCM 2023) for Martha's Vineyard and Nantucket

	Total land area (km ²)	Population density (people km ⁻²)	Forest (%)	Agriculture (%)	Developed (%)	Grassland (%)	Shrub/scrub (%)	Fresh-water (%)
Long Island (Suffolk)	2362	631.5	29.2	7.1	54.6	1.4	0.5	3.4
Long Island (east end)	901	154.3	38.7	15.2	34.5	2.6	0.8	3.4
Martha's Vineyard	227	69.4	58.9	4.6	14	6.2	9.2	1.9
Nantucket	121.5	115.1	9.7	2.1	19.4	17.5	32.3	8.4

sampling on Long Island and 25 each on Martha's Vineyard and Nantucket, with an attempt to sample an equal number of units in each canopy cover category; however, units in the highest canopy cover categories were limited on the smaller islands, resulting in an uneven distribution (Fig. 1). Within selected sampling units, we surveyed 3 random sites, with each site located >200 m from others within the unit following USFWS-recommended summer survey guidelines for acoustic detector placement (USFWS 2023a). Survey sites were located on both public and private lands, and if permission to access a private site was denied, then we moved to the closest property until permission was granted.

2.3. Acoustic surveys

We used full-spectrum ultrasonic detectors (SM4 BAT-FS with SMU1 or SMU2 microphones [Wildlife Acoustics] on Martha's Vineyard and Nantucket; SM4BAT-FS and iFR-IV systems with AR124 micro-

phones [Binary Acoustic Technology] on Long Island) to conduct passive acoustic surveys following standard guidelines (USFWS 2023a). All detectors were set to record from 30 min before sunset to 30 min after sunrise. SM4BAT detectors were programmed to record with a sampling rate of 256 kHz, a minimum signal duration of 1.5 ms with no maximum signal duration, a trigger level of 12 dB, a minimum trigger frequency of 16 kHz, and a maximum recording length of 15 s. We elevated each microphone at least 1.5 m off the ground (or above ground vegetation) positioned to minimize clutter within the zone of detection. In 2017, we surveyed each cell on Long Island for a 1–8 night period from 25 May to 8 October. The following year, we surveyed Martha's Vineyard and Nantucket from 22 May to 19 August 2018, visiting each cell once with detectors recording between 2 and 8 nights. Occasionally, detectors malfunctioned and only recorded for part of the night. We excluded any nights with partial recordings due to detector malfunction or poor weather from analysis.

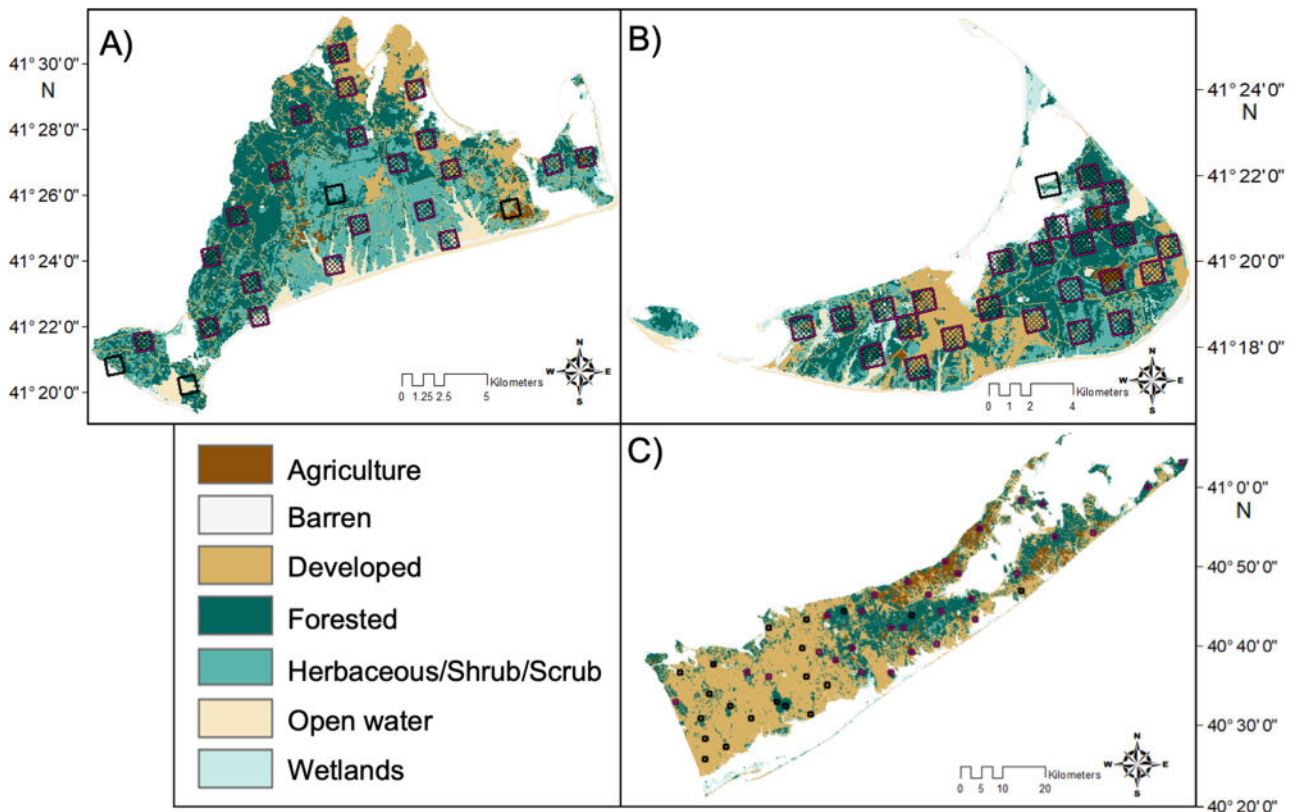


Fig. 1. Acoustic survey locations and naïve occupancy results of northern myotis *Myotis septentrionalis* for the islands of (A) Long Island (2017), (B) Martha's Vineyard (2018), and (C) Nantucket (2018). Maps show land cover of our study area obtained from the 2016 National Land Cover Dataset (Dewitz & USGS 2019) and the 2016 C-CAP Land Cover Massachusetts Land Cover/Land Use Dataset (OCM 2023). Squares: the grid cells sampled; squares with crosshatching and pink outlines: presence of northern myotis

2.4. Detection covariate sampling

Given that bat activity has been shown to vary with weather conditions (Patriquin et al. 2016, Gorman et al. 2021), we considered the effect of 2 weather covariates on detection: minimum nightly temperature and mean nightly wind speed. Weather covariates were averaged from hourly observations at the closest weather stations to our sampling sites (<https://www.ncei.noaa.gov/metadata/geoportal/rest/metadata/item/gov.noaa.ncdc:C00684/html>). To account for potential changes in detection due to seasonal movements and volant juveniles on the landscape after mid-July, we tested survey date as a linear covariate (date) and quadratic covariate (date²). Additionally, we assessed whether the use of 2 types of acoustic detectors affected detection probability on Long Island by including detector type (SM4 or BAT; detector type) as a covariate for this study site.

2.5. Occupancy covariate sampling

We used ArcGIS 10.7 to derive a number of metrics to reflect patterns of land cover and forest patch dynamics at local (site) and landscape (unit) scales. Landscape-scale environmental associations were evaluated based on units of 1 km² grid cells. This unit size is appropriate for encompassing average home range sizes of approximately 60–70 ha and average summer movement distances between roosts (<0.8 km) reported in the literature (Owen et al. 2003, Lacki et al. 2009, Silvis et al. 2016). For local-scale factors affecting occupancy, we evaluated 7 variables within 200 m circular buffers around sampled sites. The minimum roosting area of maternity colonies varies greatly depending on habitat contiguity, with estimates ranging from 0.3 to 88.4 ha (Henderson & Broders 2008, Gorman et al. 2022a); therefore the 200 m buffer represents an average minimum roosting area. Because home-range sizes for northern myotis are larger than the spacing between our sampled sites, results may be interpreted as relative habitat use at the local scale (Thomas et al. 2019). Covariates were estimated using the 2016 NLCD (Dewitz & USGS 2019) for Long Island and the 2016 C-CAP Land Cover Massachusetts Land Cover/Land Use Dataset (OCM 2023) for Martha's Vineyard and Nantucket. For covariates on landscape-scale occupancy, we combined the land cover categories into 6 broad land cover types: canopy cover (both deciduous and evergreen forest), forest, agriculture,

grassland/shrubland, freshwater, and impervious surface to represent development. In addition, we measured mean forest patch size (MPS) and edge density (forest area/edge length; EdgeD) within each unit to represent landscape structure. For covariates on local-scale occupancy, we refined the broad-scale land cover types into subcategories representing fine-scale land cover (forest, agriculture, grassland, shrubland, freshwater, development, open development). We measured Euclidean distance to features of importance that could negatively affect local occupancy (forest edge) or positively affect local occupancy (freshwater wetlands) in meters. All land cover covariates were converted to the proportion of each habitat type within the grid cell or 200 m buffer, and we normalized all continuous covariates to improve model convergence and interpretability.

2.6. Data analysis

We used analysis software to process all recordings (Kaleidoscope Pro, Wildlife Acoustics, version 4.3.0; Classifier version: Bats of Eastern North America 5.4.0, –1 Sensitivity Setting; see our Table S1a in the Supplement at www.int-res.com/articles/suppl/n054p141_supp.pdf). The range of Indiana bats *Myotis sodalis* and small-footed bats *M. leibii* does not encompass our study area and there are no known records from the islands, so these 2 species were excluded from possible auto-classification. There are no records of little brown bats *M. lucifugus* on Nantucket, and this species was present on Long Island and Martha's Vineyard prior to the arrival of WNS (although they did not appear to constitute a significant portion of the bat community; Connor 1971, Buresch 1999), but both populations have since been reduced to near extirpation, thus reducing the likelihood of recording little brown bat calls (1 actively monitored maternity colony remains on Martha's Vineyard, and no little brown bats have been captured on Long Island in post-WNS years). Additionally, we placed microphones in areas with minimal clutter to maximize recording quality and reduce potential ambiguity of *Myotis* spp. echolocation calls (Broders et al. 2004), and we manually vetted all recordings identified as northern myotis, little brown bat, NoID/Noise to ensure that no northern myotis calls were misclassified (Table S1b). Our manual vetting process is as follows: (1) assess call sequence quality (only recordings with search phase calls that contained ≥ 3 pulses and those with signals that rise above the back-

ground level noise), and (2) examine entire call sequence and characteristics of individual pulses. The characteristics we used to identify northern myotis calls were the following: pulses with terminal slopes ≥ 150 , a large bandwidth up to 100 kHz within a short pulse duration (average: 3.9 ms), and a minimum frequency of ≥ 35 kHz.

We used the package 'RMark' to develop separate single-season, multi-scale occupancy models for each study area (Laake 2013). Multi-scale occupancy models offer a hierarchical design that allows for simultaneous analysis at 2 spatial scales: the landscape scale (species use of a sample unit) assesses landscape factors affecting occupancy, and the local scale (species use of a sample site) assesses local factors affecting occupancy (Nichols et al. 2008). This approach addresses the spatial component of closure assumption for replicated survey sites within the landscape sample units (Pavlacky et al. 2012) and accounts for the lack of independence of detections between scales while also utilizing this dependence to permit inference about occupancy at both spatial scales (Nichols et al. 2008). The model parameter p is the probability of detecting a species during sampling occasion t , given that the species is present at the immediate sample site. At the landscape (1 km² sampling unit) scale, we estimated the probability that the species is present, and the unit is used, defined as occupancy (ψ). The probability that a species used a survey site at the local scale (200 m buffer, defined as θ) is conditional on it being present at the landscape scale and detected during a sampling occasion (t) (Nichols et al. 2008, Mordecai et al. 2011). Each detector night of recording represents an independent survey, and from these data were created nightly presence–absence detection histories to estimate p from repeated surveys.

The naïve estimate of occupancy is the proportion of sites where northern myotis were detected, and this estimate will be biased low if detection is imperfect (MacKenzie et al. 2002). Given that our naïve occupancy estimates were between 70 and 94%, we took a 'step-down' approach to model selection (Lebreton et al. 1992). We first fit models for p , then θ , then ψ , retaining covariates from the top-ranked models at each step in the modeling process (those within 2 Δ AIC units, where Δ AIC is the difference in Akaike's information criterion [AIC] values compared to the top-ranked model; Burnham & Anderson 2002). To avoid over-parameterization, only 1 covariate for each occupancy measure (ψ and θ) was included for any given model, and not all proposed covariates at the landscape or local scale were used for model sets

on each island due to lack of representation of that covariate within our units or sites (Table S2). We evaluated support for competing models at each step using corrected AIC (AIC_c) and associated model weights (Burnham & Anderson 2002), and we considered covariates to have a significant relationship with each model parameter if the confidence intervals did not overlap zero. Due to high levels of model uncertainty, we used model averaging to increase precision and minimize bias of parameter estimates (Burnham & Anderson 2002). Additionally, we ran models for each island with p varying by survey night ($p^* = 1 - (1 - p)^t$) while holding ψ and θ fixed at their best-supported model structures to determine t , the number of survey nights required to achieve a 90% probability of detecting northern myotis at least once while present, to guide future monitoring efforts.

3. RESULTS

A total of 221 575 acoustic recordings were assessed over 954 recorder nights, and from these data we manually identified 8098 recordings as northern myotis (3% of the total bat recordings on Long Island, 7% on Martha's Vineyard, and 84% on Nantucket; Table S1). Northern myotis were detected on 30% of sample nights on Long Island, 37% of nights on Martha's Vineyard, and 70% of nights on Nantucket. Without accounting for imperfect detection, naïve occupancy estimates of northern myotis were 70, 70, and 94% at the local scale and 62, 84, and 96% at the landscape scale for Long Island, Martha's Vineyard, and Nantucket, respectively. Of the sites we surveyed across all 3 study areas ($n = 280$), the majority were within forested patches of ≤ 250 ha (81%), and patch area had no effect on naïve occupancy, as a relatively similar magnitude of sites with forest patches of ≤ 0.5 or ≥ 250 ha were occupied on each island (64 vs. 56%; Fig. 2A, Table S3). Northern myotis were present in sampling units of all canopy cover levels (Fig. 2B) and those with a proportion of development ranging from 0.0 to 0.94 (median values, Long Island = 0.45, Martha's Vineyard = 0.04, Nantucket = 0.10).

3.1. Detection probability

On Long Island, the null model of detection ranked highest. Models including mean nightly wind speed and date were within 2 Δ AIC_c of the null model, but these relationships were not significant (Tables S2 & S4). The highest ranked model of detection for Nan-

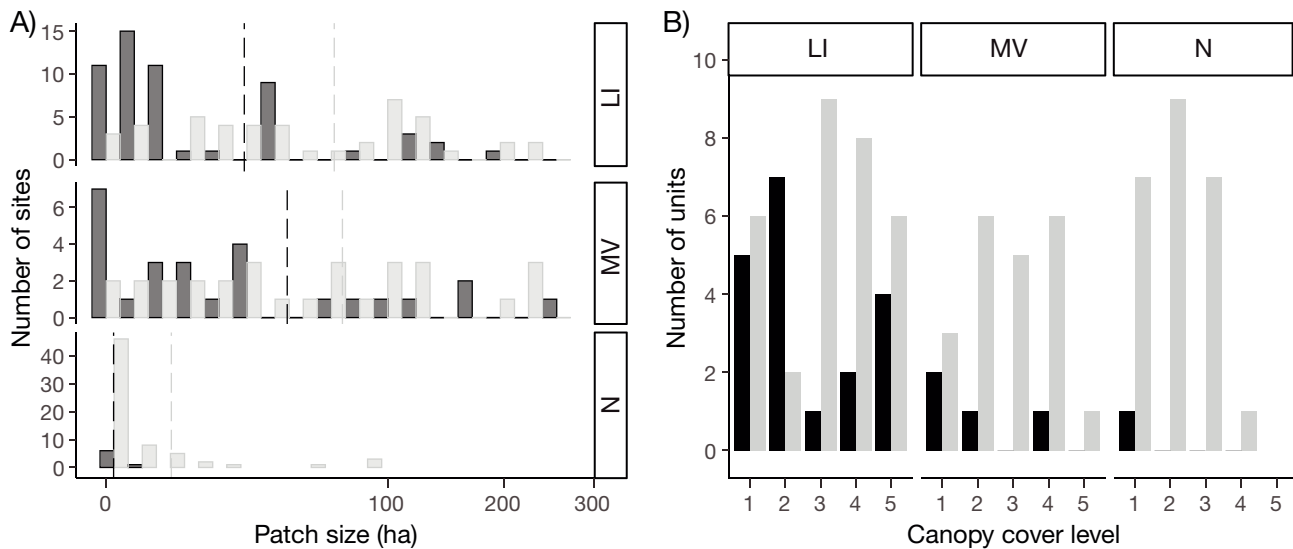


Fig. 2. Detection (light grey) and non-detection (dark grey) of (A) northern myotis *Myotis septentrionalis* within sampled forest patches (square root-transformed) at the local occupancy scale, and (B) landscape-scale occupancy (ψ) of northern myotis survey cells based on canopy cover level for Long Island (LI), Martha's Vineyard (MV), and Nantucket (N). (A) Vertical dashed lines: the average patch size for detection and non-detection sites. (B) Canopy cover is separated into 5 percentage categories (1 = 0–20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–80%, 5 = 81–100%)

tucket had an AIC_c weight of 83% and included date² (Fig. 3A) and mean nightly wind speed (Fig. 3B, Table S2), with an inverse relationship between detection probability and both covariates (Table S4). The null model of detection ranked highest on Martha's Vineyard, and while models including date, date², and the minimum nightly temperature fell within 2 ΔAIC_c of the null model (Table S2), these relationships were not significant (Table S4). Detection probabilities for 1 survey night estimated from our time-varying models were lowest on Long Island ($\hat{p} = 0.52$, SE = 0.06) and highest on Nantucket ($\hat{p} = 0.74$, SE = 0.03), while Martha's Vineyard fell in the middle ($\hat{p} = 0.54$, SE = 0.05). Survey nights (p^*) needed to achieve a detection probability of $\alpha = 0.90$ were 2 nights on Nantucket and 3 nights on Long Island and Martha's Vineyard (Fig. 3C).

3.2. Local-scale occupancy

The top-ranked models at the local scale for Long Island contained the proportion of development within a 200 m buffer, and these models had a combined AIC_c weight of 100% (Table S2). Local occupancy significantly decreased with increasing proportion of development within 200 m of the survey site (Fig. 4A, Table S4; $\hat{\beta} = -4.51$ [95% CI: -6.47 to -2.56]), and the average proportion of sites occupied across the study area was estimated to be 0.60 (SE =

0.07). Occurrence at the local scale on Martha's Vineyard was best explained by the top model that included the proportion of forest within 200 m (Fig. 4B, Table S2; $\hat{\beta} = 3.40$ [1.08 to 5.72]) and estimated the average proportion of sites occupied as 0.68 (SE = 0.09). Probability of occupancy increased as the proportion of forest increased (Table S4). The highest-ranked model on Nantucket described an inverse relationship between the proportion of open development within 200 m and local occupancy (Fig. 4C, Table S4; $\hat{\beta} = -4.45$ [-8.52 to -0.37]), although this model only had an AIC_c weight of 49% (Table S2). The naïve site occupancy on Nantucket (0.94) was slightly lower than the model estimate (0.98, SE = 0.02).

3.3. Landscape-unit scale occupancy

For each island, none of the covariates we measured had strong relationships with landscape-scale occupancy for northern myotis within our study area. Both mean patch size and canopy cover had an overall negative influence on occupancy for Long Island, while forest habitat had a positive influence on occupancy for Martha's Vineyard, but relationships were not significant (Table S4). The model-averaged estimates of landscape-scale occupancy were $\hat{\psi} = 0.81$ (SE = 0.09) on Long Island, $\hat{\psi} = 0.97$ (SE = 0.09) on Martha's Vineyard, and $\hat{\psi} = 0.96$ (SE = 0.04) on Nantucket.

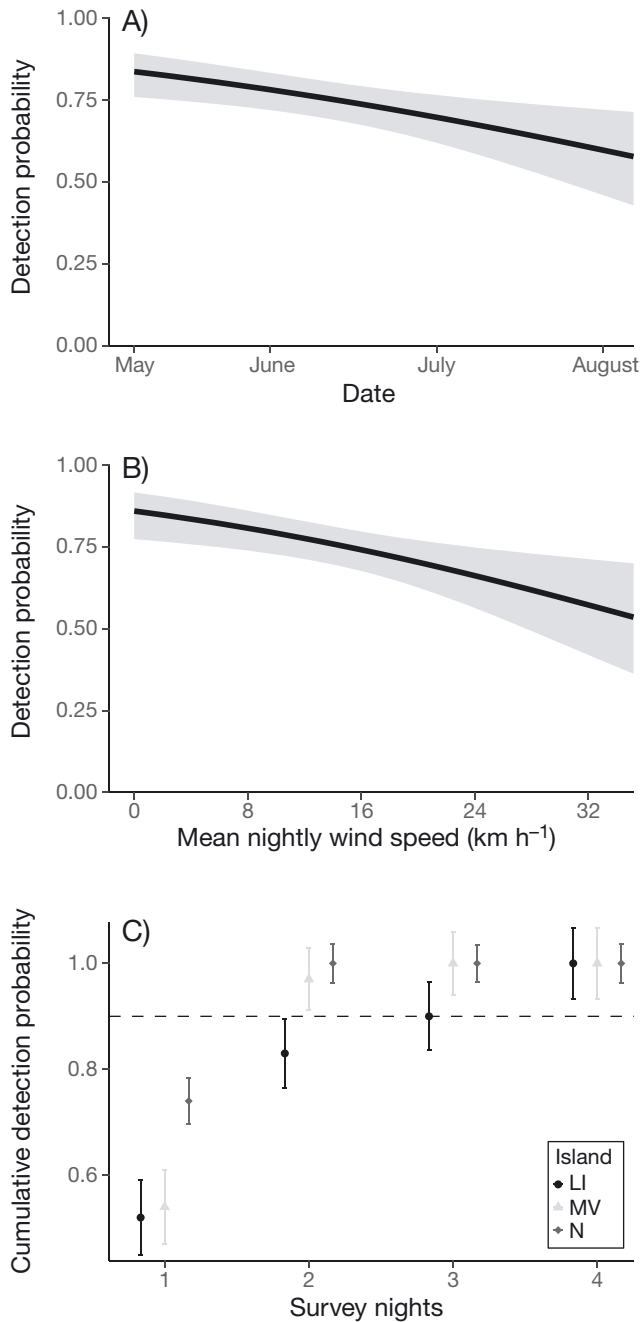


Fig. 3. Association between (A) date² and (B) mean nightly wind speed and the detection probability of northern myotis *Myotis septentrionalis* acoustically surveyed on Nantucket from May to August 2018. Solid black lines represent the model predicted covariate effects; grey shading: 95% CIs. Detection probabilities on Long Island and Martha's Vineyard did not have any significant associations with the tested covariates. (C) Estimated detection rates of northern myotis by number of survey nights (LI: Long Island; MV: Martha's Vineyard; N: Nantucket). Dashed horizontal line: 90% likelihood that northern myotis will be detected if they are present; error bars: SE. Survey nights needed to achieve a detection probability of $\alpha = 0.90$ were 2 nights on Nantucket and 3 nights on Long Island and Martha's Vineyard

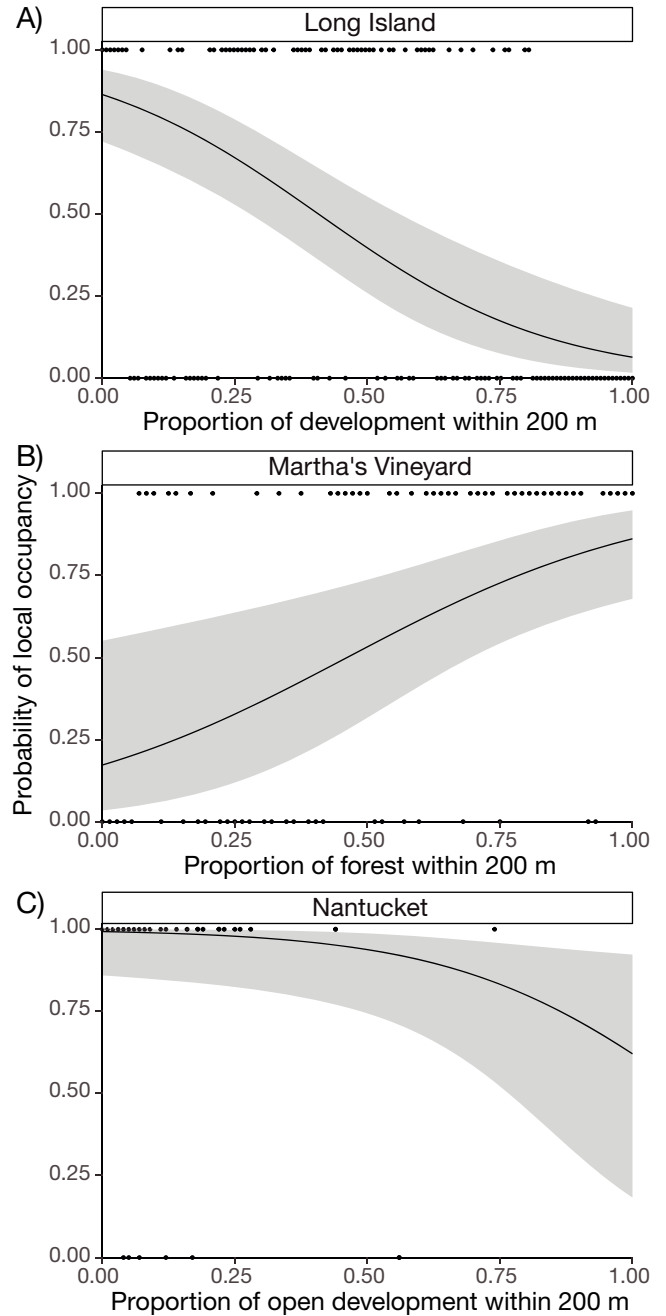


Fig. 4. Association between northern myotis *Myotis septentrionalis* local-scale occupancy (θ) and the proportion of (A) development on Long Island, (B) forest on Martha's Vineyard, and (C) open development on Nantucket within 200 m of our survey locations. Solid black lines represent the model predicted covariate effects; black points show the naïve occupancy at each survey location; grey shading: 95% CIs. Local occupancy decreased as the proportion of development on Long Island or open development on Nantucket increased, and local occupancy increased with a greater proportion of forest on Martha's Vineyard. Martha's Vineyard and Nantucket were acoustically surveyed in May–August 2018 and Long Island in May–October 2017. Local occupancy was estimated to be 0.60, 0.68, and 0.98 on Long Island, Martha's Vineyard, and Nantucket, respectively

4. DISCUSSION

Despite range-wide population declines of northern myotis in post-WNS years, our estimates of occupancy and detection probability suggest widespread presence across 3 islands within the northeastern Atlantic Coastal Plain. None of the variables we measured adequately explained the landscape occupancy of this species on Long Island, Martha's Vineyard, and Nantucket, which may be due to the high naïve occupancy estimates on each island. Local occupancy rates were influenced by either the amount of development, open development, or forested habitat surrounding our sampling locations; however, we did not find a relationship between occupancy and habitat variables commonly associated with this species, such as riparian (Pauli et al. 2017, Gorman et al. 2022b) or edge habitat (Perry et al. 2008, Gorman et al. 2022b). While occupancy is typically limited at the periphery of a species range due to variable abiotic and biotic conditions compared to the core (Munwes et al. 2010), these same factors that provide environmental heterogeneity may facilitate greater fitness and plasticity through adaptations to local conditions (Valladares et al. 2014, Zettlemyer & Peterson 2021). These processes may be particularly important for island populations that are exposed to human-driven habitat alteration, as their population size is restricted by limited space and resources (Ancillotto et al. 2021). Our findings highlight the importance of assessing factors of localized relevance to the occurrence of endangered species to account for hierarchical habitat selection in response to the diversity of threats facing populations.

Detection probabilities of northern myotis on the islands were orders of magnitude higher than those reported from similar acoustic studies encompassing the northeast and other portions of the species range post-WNS (Grider 2016, Pauli et al. 2017, De La Cruz et al. 2019, Deeley et al. 2021), suggesting that robust populations remain on each island. In a study of occupancy across the northeast, De La Cruz et al. (2019) estimated the highest detection probability of this species to be $p = 0.23$ within the North Atlantic Coast ecoregion, which covers a large geographic range that encompasses our study region, while our estimates ranged from $p = 0.52$ – 0.74 for 1 survey night on the islands. Higher detection rates on the island may be due to the lack of other *Myotis* spp., which are notoriously difficult to distinguish (Britzke et al. 2013), facilitating greater confidence in identification of acoustic re-

cordings. Additionally, manual vetting of acoustic recordings resulted in additional northern myotis identifications that may otherwise have been misclassified. Regardless, mainland populations within the core of the species range have declined precipitously, whereas we have documented persistence of these peripheral northern myotis populations up to 10 yr after WNS arrival, indicating that this region may be serving as refugia to promote survival. We recognize that our results are an anomaly in the post-WNS world, and given the variety of environmental processes that limit a species range (e.g. climate, habitat, and bat community differences that may limit abundance), we would not expect all peripheral populations of northern myotis to serve as refugia.

Two variables that are commonly associated with bat activity, i.e. mean nightly wind speed and day of the year, were included in many of our top-ranked detection models; however, the strongest relationships occurred on Nantucket. Detection probability was inversely related to wind speed and day of the year, although there remained a >50% chance of detecting northern myotis at the end of our sampling period in mid-August and on nights when the highest wind speeds were recorded. Greater detections during June and July likely represent an increase in concentrated foraging activity and roost switching by reproductive females (Patriquin et al. 2016, Deeley 2019), while the subsequent decline in detection coincides with the onset of juvenile volancy and dissolution of maternity colonies after the reproductive window ends (Lacki & Schwierjohann 2001, Gorman et al. 2022b, Lewis et al. 2022). While our results support the nearly universal negative association between bat activity and wind speed (Reynolds 2006, Johnson et al. 2011), Nantucket bats remained active on the landscape on nights with average wind speeds as high as 22 mph (35 km h^{-1}). Nantucket experiences higher wind speeds relative to our other study areas as it is the furthest island offshore with the least amount of forest cover, and thus individuals may have adapted to flying in higher wind speeds than would be expected elsewhere. The lack of a strong relationship between wind and detection on the other islands may be due to wind speed measurements generated from central locations on each island that are not representative of site-specific conditions with greater canopy cover that would provide a buffer against wind.

Commonly described as a forest-dwelling species, the strong association between northern myotis occupancy and forest habitat on Martha's Vineyard was expected, but surprisingly this relationship was not

observed across all islands. In general, forest conditions differ within and among the islands due to past disturbance regimes and current land use and management practices. Martha's Vineyard has the highest percentage of island-wide forest cover among our study sites, which may result in fewer constraints on availability of preferred habitat. In contrast to our predictions that occupancy would be positively associated with patch size, we found no relationship between the two, and northern myotis occupied forest patches as small as <0.5 ha, demonstrating that this species can utilize disturbed or non-contiguous forest patches near intense urban development (Thorne et al. 2021, Gorman et al. 2022a, Hoff et al. 2024). Northern myotis often select forested habitat frequently altered by small-scale disturbances that create more roosts or enhance existing roost quality (De La Cruz et al. 2019), although there is likely a limit to this tolerance. This delicate balance has strong implications for conservation of this species along the coast where preferred habitat is limited, and remaining areas of continuous interior forest are rare and rapidly under the threat of development pressure.

Contrary to our predictions, we did reveal a strong negative effect of development on local occupancy for Long Island. This suggests that while northern myotis may roost opportunistically in urban areas on the edge of forest habitat (Gorman et al. 2022a, Hoff et al. 2024), other essential behaviors such as foraging are concentrated in forested patches, and thus we see greater occupancy in areas surrounded by less development. Interior forest habitat offers a refuge from anthropogenic stressors in urban landscapes such as noise and artificial light pollution (Siemers & Schaub 2011, Rowse et al. 2016), which may result in decreased foraging activity due to increased predation risk and decreased prey abundance (Threlfall et al. 2012). Likelihood of local occupancy on Nantucket remained >50% even with a high proportion of surrounding open development (characterized by <20% impervious surfaces, mostly vegetation in the form of lawns, parks, golf courses, and large-lot housing units). This trend may reflect local adaptations of northern myotis in response to the limited forest habitat on this island, such as the use of suboptimal habitats for essential behaviors.

Our multi-scale modeling approach indicates that northern myotis may be more sensitive to site-specific habitat conditions that drive fine-scale habitat selection. As a result of widespread occupancy across each island, none of the covariates measured at the landscape scale explained the distribution of northern myotis on the islands. In contrast to our predictions

that occupancy would be positively related to canopy cover, northern myotis were present in units of all canopy cover levels that had representation of all measured land cover types, which may be why we failed to find significant effects of any landscape-scale environmental influences. Recent studies have documented remnant populations not just along the coast but also within isolated regions throughout the core of the species range (De La Cruz et al. 2019, Lewis et al. 2022, Garcia et al. 2023), and a comparison of northern myotis activity between interior and coastal areas (including a site on Long Island) indicated no difference between the 2 regions (Gorman et al. 2022b). In concert with our findings, these results suggest that broad land cover may not be a driving factor explaining higher occupancy of populations in coastal areas if peripheral habitats are not inherently different from core habitats, and that there may be other biotic or abiotic factors influencing population persistence and reducing disease severity. Future research could conduct analyses at additional spatial scales and incorporate more localized measures of habitat conditions and fragmentation metrics to reveal additional environmental associations on occupancy.

Understanding the processes driving the regional distribution of endangered species is a primary step to inform management of populations of conservation concern, and our study is the first to directly investigate the distribution, detection patterns, and environmental associations of persisting northern myotis populations on islands of the northeast Atlantic Coastal Plain. A multi-scale approach is useful for monitoring hierarchical habitat use by linking the response of populations to differences in habitat across multiple scales (Pavlacky et al. 2012), whereas modeling occupancy at only 1 scale can result in bias, or it may not be sensitive enough to detect declines due to environmental changes as they begin to influence distributional patterns. Additionally, multi-scale occupancy may reveal fine-scale habitat associations most relevant to the variety of stakeholders managing land across regions with persisting populations, and allow for the prioritization of conservation efforts at the local scale. Multi-scale occupancy models have recently been extended to incorporate dynamic parameters that provide insight into the mechanisms driving species distributions over time (Green et al. 2019), such as turnover rates between patches of varying habitat suitability. Data from our study could serve as a baseline and be incorporated into a long-term monitoring plan that utilizes dynamic multi-scale models to assess potential changes in occupancy or detection

resulting from threats such as WNS and future land-use change (Neece et al. 2018, Hyzy et al. 2020). While our estimates of detection indicate the federal survey guidelines for this species are more than adequate for determining presence/absence within our study area (USFWS 2023a), we caution the extrapolation of our results to other regions. It may be prudent to generate power estimates, conduct exploratory surveys, and incorporate location-specific detectability into study sample design to consider the differing levels of effort that may be needed to achieve specific study objectives (Deeley 2019).

A one-size-fits-all approach to managing landscapes across the species range would overlook the potential behavioral plasticity in response to local conditions, and our results suggest that a thorough review of the proposed guidance designed to minimize impact to northern myotis, particularly restrictions for habitat modification that are based on patch size (USFWS 2023b), can aid conservation efforts. Additionally, our observations of bat activity in conditions above the recommended threshold for wind turbine cut-in speeds has implications for the planned expansion of wind energy in the nearshore and offshore environments along the Atlantic Coast to meet renewable energy objectives (Solick & Newman 2021, EERE 2022). Although our estimates of occupancy and detection indicate robust populations remain on the islands, the viability of persisting populations in supporting species survival is unknown, and further monitoring may elucidate long-term trends. Future studies could continue acoustic surveys and incorporate tracking efforts into monitoring protocols to gain further insight into population-level survival and reproduction, in addition to investigating biotic and abiotic factors that may be mediating host–pathogen interactions within coastal landscapes. Additionally, our approach could be applied to other persisting northern myotis populations along the entire Atlantic Coastal Plain to better understand localized impacts of anthropogenic threats and may be applicable to additional species of concern that occur at the edges of their geographical range.

Acknowledgements. We acknowledge the Martha's Vineyard Landbank, Massachusetts Department of Conservation and Recreation, Sheriff's Meadow Foundation, New York State (NYS) Office of Parks, Recreation and Historical Preservation, Suffolk County Parks, and the generous private landowners for providing access to sites for sampling. Additionally, we thank Jeff Laake for providing his software and modeling expertise, and our peer reviewers for helpful comments that improved the quality of the final manuscript. Any use of trade, firm, or product names is for de-

scriptive purposes only and does not imply endorsement by the US Government. At the time of publication, the data that support the findings of this study were not available from the NYS Department of Conservation or the Massachusetts Division of Fisheries and Wildlife (MassWildlife). Data may be made available from the corresponding author (S.H.) or either supporting organization, upon reasonable request.

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Editorial responsibility: Alexandros A. Karamanlidis,
Thessaloniki, Greece
Reviewed by: 3 anonymous referees

Submitted: September 13, 2023
Accepted: April 9, 2024
Proofs received from author(s): June 3, 2024