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Cover Photograph: The charming and elusive Northern long-eared Bat (*Myotis septentrionalis*) often roosts in crevices where they can be difficult to spot. This species was once common throughout North America but has recently faced precipitous population declines largely due to white-nose syndrome. © Jill Utrup/USFWS.

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Multi-scale Predictors of Northern Long-eared Bat (*Myotis septentrionalis*) Occupancy in the United States

Amy K. Wray[1,*], Bradley J. Udell[1], Helen T. Davis[1], Richard D. Inman[1], Bennet T. Lohre[1], Haley B. Price[1], Jonathan D. Reichard[2], Andrea N. Schuhmann[1], Bethany R. Straw[1], Frank C. Tousley[1], Jill Utrup[2], Ashton Wiens[3], and Brian E. Reichert[1]

Abstract - Historically, *Myotis septentrionalis* (Northern Long-eared Bat) was among the most common forest-interior species in North America. Largely due to high mortality from white-nose syndrome, this species has experienced severe population declines across its range. To create an updated species distribution map representing summer occupancy probabilities from 2017 to 2022, we integrated stationary acoustic data with live-capture data from the database of the North American Bat Monitoring Program into a multi-scale, multi-method occupancy modeling framework. Our results provide data-driven predictions with quantified uncertainty for summer occupancy probabilities for Northern Long-eared Bats at 2 spatial scales across the range of the species, while also accounting for inherent observation biases (e.g., imperfect detection).

Introduction

Efficient wildlife management requires understanding where the species of interest likely occurs. Predicting occurrence for populations in decline is challenging—even more so for species that are small, cryptic, or highly mobile (Emmet et al. 2021; MacKenzie et al. 2002, 2005). For species that are rare and challenging to survey, traditional modeling methods often require extensive data collection and intensive modeling frameworks (Balantic and Donovan 2019, MacKenzie et al. 2002, Nichols et al. 2008). Multi-scale models can offer solutions for predicting the occurrence of species with low detection probability by using sampling units to explicitly account for both the spatial (availability bias) and temporal (perception bias) components of imperfect detection (Nichols et al. 2008). Multi-scale and multi-method models allow for the incorporation of data collected at various spatial scales or using different methods, thereby maximizing the amount of information used to calibrate a model. Some understanding of the resources that govern the distribution of a species is also required to make predictions that are ecologically meaningful. Adding this valuable context can be achieved through the inclusion of model covariates informed by the natural history of a species.

Myotis septentrionalis (Trouessart) (Northern Long-eared Bat) is widely distributed across North America (U.S. Fish and Wildlife Service 2022a). Compared to many other *Myotis*, this small-bodied species has low wing loading and is adapted to moving and foraging in forest understories (Caceres and Barclay 2000). Since Northern Long-eared Bats forage by aerial hawking in cluttered environments, as well as by gleaning prey, their search-phase echolocation calls are quiet and generally higher in frequency, steeper in slope, and shorter

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in duration compared to sympatric species, although these characteristics can shift depending on the vegetation structure present in their environment (Broders et al. 2004, Faure et al. 1993). Though previously common throughout their range, recent capture rates of Northern Long-eared Bats are low (Rojas et al. 2019), and these bats can be difficult to observe in hibernacula or distinguish from other *Myotis* due to their preference for hibernating in deep crevices or cracks (Raesly and Gates 1987). Since the arrival of the fungal disease white-nose syndrome (WNS) in North America, this species has been one of the most severely afflicted, with population declines ranging from 97 to 100% (Cheng et al. 2021, Frick et al. 2015). The severe declines have led to the species being classified as endangered in the United States (U.S. Fish and Wildlife Service 2022b).

Strategic modelling efforts can support conservation and management decisions for wide-ranging species with varying data availability, as is the case for Northern Long-eared Bats. For other taxa, centralized systems for managing large datasets, such as eBird (Neate-Clegg et al. 2020) and the Global Biodiversity Information Facility (Svenningsen and Schigel 2024), have facilitated population-monitoring on a broader scale than previously possible. However, for many bats, standardized landscape-level data that could enable these types of analyses have been limited until recently. Largely due to the adoption of acoustic-monitoring techniques, the quantity of available monitoring data on bats has increased substantially (Sugai et al. 2019). The North American Bat Monitoring Program (NABat) was created, in part, to expand acoustic and non-acoustic data collection for bats (Loeb et al. 2015, Reichert et al. 2021). NABat also aims to increase accessibility to those data to inform timely decisions for managing bats (Neece et al. 2019). Although the inherent shortcomings of acoustic autoclassification (e.g., Lemen et al. 2015, Russo and Voigt 2016) necessitate either reduction of false-positive detections (Britzke et al. 2002) or explicit modeling of false positives (e.g., Irvine et al. 2022), the large amount of data compiled through the NABat database provides unique opportunities for improved quantification of occupancy probabilities, even for species that are rare or difficult to detect. Herein, we used both capture records and data from stationary acoustic monitoring to create an updated map of occupancy probabilities across the range of the Northern Long-eared Bat in the contiguous United States. Overall, our results provide estimates of predicted occupancy probabilities for Northern Long-eared Bats that could help inform future management objectives.

Methods

Data sources

The NABat sampling scheme is based on grid cells that are 10 kilometers (km) by 10 km (hereafter called grid cells), each of which includes 4 nested quadrants of 5 km by 5 km (hereafter called quadrants). Model inputs included data collected in summer (1 May through 31 August) from 2012 through 2022, with predictions made only for the pre-volancy season (1 May through 15 July; Loeb et al. 2015). We performed data processing, quality inspection, and formatting in R version 4.3.2 (R Core Team 2023) with the specific packages “tidyverse” and “sf” (Pebesma 2018, Wickham et al. 2019). For clarity, we have shown the general workflow for data inclusion in the occupancy model in Figure 1. We describe the processing steps below, and more details appear in the data release of model outputs associated with this manuscript (Wray et al. 2024).

Data sources included nightly detection and non-detection records from captures and stationary acoustic surveys (hereafter “acoustic surveys”; Fig. 1). Capture records were exported from the NABat database as nightly summaries (i.e., the number of captures per species for each night of a survey). From these records, we imputed zeroes (non-detections) for surveys if other bats were captured but Northern Long-eared Bats were not caught. Acoustic records were exported from the NABat database at the level of the call file (i.e., each acoustic recording and its assigned identification) for all records using a species list (i.e., a classifier) that included the Northern Long-eared Bat.

For acoustic survey data with manual vetting (identifications manually assigned by experts), we used the manually provided identification to determine detections and non-detections. For any call files that underwent manual vetting within the same batch of recordings, with "batch" defined as a unique combination of site, night, project, processing software, species list, and recording equipment, we used the identities assigned to the vetted records instead of relying on any automatic identifications generated by classification software (hereafter "auto IDs", Fig. 1). For example, if a subset of acoustic files in a batch received manual vetting, we excluded any remaining files from that batch that were not manually reviewed (Fig. 1). For files with manual vetting, we considered all software types (including files that did not list a software type) acceptable. Similarly, we considered files that were ambiguously identified only as "high frequency", "low frequency", or "*Myotis* spp." (Table 1) to represent a nontarget species (i.e., any bat besides the Northern Long-eared Bat).

For acoustic survey data from batches without any manual vetting, we used a maximum likelihood estimator (MLE; Britzke et al. 2002), which represents an efficient approach to maximize the amount and quality of the data inputs for our model. This approach can be useful for reducing potential false positives. Specifically, the likelihood of a species' presence

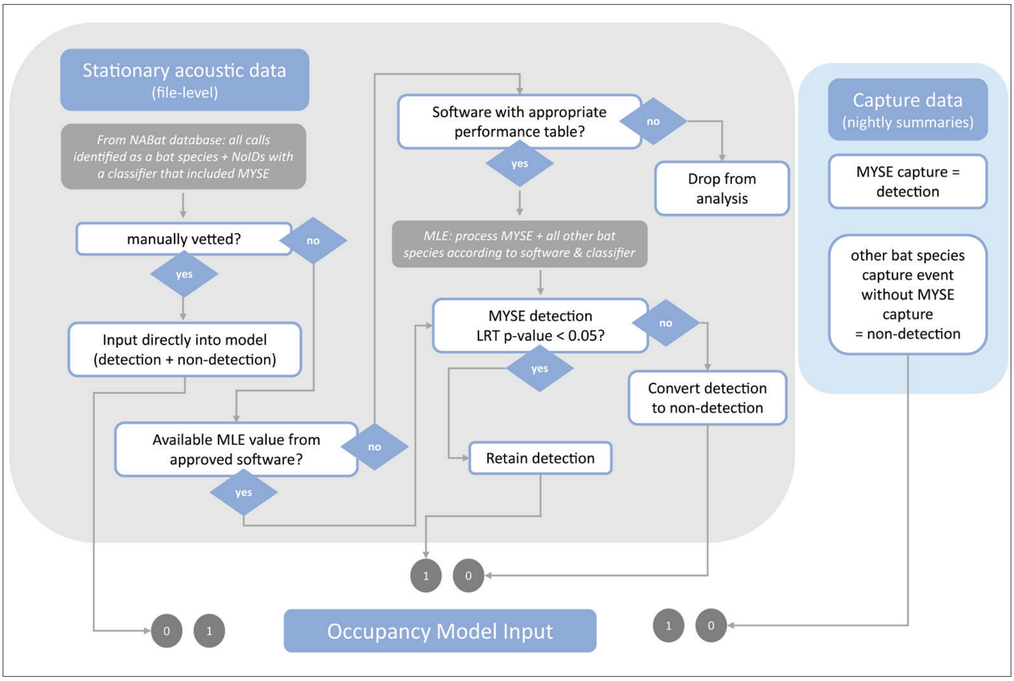


Figure 1. Decision flowchart for inclusion of stationary acoustic and capture data. Zeroes represent non-detections, while ones represent detections. MYSE = *Myotis septentrionalis* (Northern Long-eared Bat). NABat = North American Bat Monitoring Program. LRT = likelihood ratio test. MLE = maximum likelihood estimator. NoID = acoustic recording files that were identified as a bat, but not assigned to a group or user-defined category.

can be calculated depending on 3 factors—the specificity and sensitivity of a particular type of autoclassification software, the potential species included in the autoclassification species list, and the total number of auto IDs for a target species compared to all other species. Only certain software brands and versions had available performance tables that included the number (rather than the proportion or percentage) of calls that were classified as each species, which is necessary to manually calculate MLE metrics (Fig. 1). In our dataset, all versions of Kaleidoscope Pro (Wildlife Acoustics, Maynard, MA) with the version number listed had performance tables available that were acceptable for MLE calculation. Most call files from acoustic surveys without manual vetting used a software type that was compatible with manual calculation of MLE scores (see Supplemental Figure S1A, available online at https://eaglehill.us/urnaonline/suppl-files/nabr-018-Wray-s1.pdf).

MLE calculation for auto IDs from stationary acoustics without manual vetting

Performance tables for each software brand and version included individual species and the category "NoID", which represented an estimation of all files that were processed through autoclassification software but not identified to species. Since these tables did not include ambiguous groupings, like high frequency, low frequency, or *Myotis* spp. (Table 1), we excluded files with auto IDs in these categories. All species (besides Northern Long-eared Bats) and NoIDs were then aggregated into a category of "nontarget species." Approaches using MLE are imperfect. For example, true detections may be converted to false negatives, which may be more common when there are few call files from a target species or when true detections represent a low proportion of call files within the same frequency groups (Ford et al. 2024). For our approach, false negatives (but not false positives) could be accounted for by modeling the observation process (i.e., detection, described in further

Table 1. Inclusion of manual and auto ID (identifications automatically assigned by classification software) categories in model input used to create an updated bat species distribution map. MYSE = Northern Long-eared Bat (*Myotis septentrionalis*). EPFU = Big Brown Bat (*Eptesicus fuscus*). MYSEMYSO = ambiguous ID assigned as Northern Long-eared Bat or Indiana Bat (*Myotis sodalis*). 40k = various species with pulses that have a minimum frequency of approximately 35–45 kHz. HighF = various species with pulses having a minimum frequency higher than 30kHz. MYSP = unknown species in the genus *Myotis*. NoBat = not a bat. NoID = acoustic recording files that were identified as a bat, but not assigned to a group or user-defined category. MLE = maximum likelihood estimator.

Species ID in database	Description	Examples	Included in vetted data model input?	Included in MLE data model input?
1–54, 86, 90	All single bat species IDs	MYSE, EPFU	Yes	Yes
66	NoID	Unknown bat species	Yes	Yes
55–64, 72–85, 88, 94–119	All ambiguous multiple bat species IDS	MYSEMYSO	Yes	No
67–71, 92–93	Frequency categories, general species codes	40k, MYSP, HighF	Yes	No
65, 89	Noise/not a bat	Noise, NoBat	No	No

detail in the Modeling Framework section). As such, we used MLE to balance inclusion of as much data as possible while recognizing that call identifications assigned by autoclassification software can be problematic (e.g., Goodwin and Gillam 2021).

To calculate MLE scores, we used the following process. First, for each unique combination of a species list, software brand, and software version, we calculated matrices with true positive, false negative, false positive, and true negative rates based on the performance tables for each software brand and version (as described in the previous paragraph) and the species included in each species list. Second, we processed call file data from each unique combination of a species list, software type, and software version through these matrices and computed a closed-form likelihood ratio test for each nightly survey (represented by a unique combination of a survey night, survey location, detector type, microphone type, microphone height, software version, classifier/species list, and project ID). Finally, for any surveys with $P < 0.05$, indicating likely presence of the Northern Long-eared Bat at high confidence, we retained these detections, while survey events with $P \geq 0.05$ were converted to non-detections (Fig. 1). For most surveys with auto IDs that were converted to non-detections based on MLE scores, the total number of call files with auto IDs of Northern Long-eared Bats was less than 3 (see Supplemental Figure S1B, available online at https://eaglehill.us/urnaonline/suppl-files/nabr-018-Wray-s1.pdf).

Covariate extraction

Some covariates used in the analysis were previously attributed to the NABat sampling grids and quadrants in prior USGS data releases (Gaulke et al. 2023, Talbert and Reichert 2018). Details on their geoprocessing can be found in their corresponding metadata. Given the seasonal migrations of the Northern Long-eared Bat and catastrophic declines of winter populations (Cheng et al. 2021), we included the presence of karst as a grid-cell level predictor. At the quadrant level, we used the proportion of the landscape that was classified as wetlands to represent riparian and forest edge habitats that can provide key food resources and movement corridors (Kaminski et al. 2020, Gorman et al. 2022).

In addition to these spatial covariates from the attributed grids, we used a previously developed model of roost-site suitability (Inman et al. 2024), which was incorporated as a predictor of occupancy at both spatial scales. The top 3 contributors to the roost-suitability metric were canopy cover, accounting for 66.9% of the total contribution to the metric, followed by annual temperature (11.5%), and landcover entropy (9.2%). The mean importance of all covariates included in the roost-suitability metric is shown in Table 2 (refer to Inman et al. [2024] for sources and geoprocessing details). This roost-suitability metric used counts at roost emergences from the NABat database and from the U.S. Forest Service, which were incorporated into a presence-background modeling approach that employed the Maximum Entropy algorithm (Inman et al. 2024). We scaled all covariates with a "*z*-score" transformation (i.e., the sample mean, that is, the mean of all values for each covariate, was subtracted from each value and this difference was then divided by the sample standard deviation).

We calculated a seasonal population connectivity metric for each grid cell and year, per Udell et al. (2024, 2025), to link the potential spatiotemporal influence of abundance in the winter range (i.e., at all known hibernacula, including natural and anthropogenic structures) to expected occupancy in the summer range. Briefly, we calculated this metric for each grid cell and year based on metapopulation connectivity (Moilanen and Hanski 2001). These calculations were dependent on the pairwise distances between all documented winter hibernacula and grid cells, the annual winter abundance of each hibernaculum, and the mean winter-to-summer dispersal distance of the species of interest. We used an average dispersal distance of 89 km for the Northern Long-eared Bat (U.S. Fish and Wildlife Service 2022c). The connectivity metric was centered (sample mean subtracted), but not scaled using *z*-scoring for analyses. Little is known about hibernation sites used by Northern Long-eared Bats, and in a small portion of their range, they apparently do not use subterranean hibernacula. While limited to known hibernacula, the connectivity metric represented the expected link between known winter colonies and the summer distribution over time, given the annual abundance at each hibernaculum and the average migration distance of the species. We expected that this connectivity metric would have a positive influence on summer occupancy probability and would capture the spatiotemporal influence of WNS impacts on known winter colonies, as previously found for Northern Long-eared Bats (Udell et al. 2022a, b).

Climatic conditions can influence several aspects of detection probability, including bat activity, a surveyor's choice of capture nights, and even the speed at which an echolocation call travels (Goerlitz 2018, Gorman et al. 2022). To account for these potential effects, we accessed nightly weather data for each grid-cell centroid and sampling night from Daymet (https://daymet.ornl.gov/), using the "daymetr" R package (Hufkens et al. 2018). We included total precipitation, minimum air temperature, and day of year (scaled with a *z*-score transformation) as nightly detection covariates, since they have been previously shown to influence detection probability (e.g., de La Cruz et al. 2024; Udell et al. 2022a, b). To account for non-linear temporal patterns throughout each year, a quadratic effect of day of year was also included as a detection covariate. Year was adjusted such that the first year of the data was represented by 1, the second year represented by 2, and so on. Since a different observation submodel was fit for each data type, all scaling of covariates was performed separately for each data type. We also included a temporally auto-correlated year effect and a post-volancy indicator (before or after 15 July) as detection covariates.

Modeling framework

We fitted a multi-scale, multi-method occupancy model to predict the occupancy probability (probability of presence) for Northern Long-eared Bats at the quadrant scale. We chose this type of model to maximize the amount of data that could be included, since some data from the NABat database were only available at the grid-cell scale, while other data had a finer resolution allowing for assignment to a quadrant nested within a grid cell. Multi-scale models yielded occupancy (ψ) at the larger (grid-cell) scale and availability (θ)

Table 2. Covariates contributing to the suitability metric for maternity sites (Inman et al. 2024) of the Northern Long-eared Bat (*Myotis septentrionalis*).

Covariate description	Mean percent importance (%)
Tree canopy cover	66.9
Annual temperature	11.5
Landcover entropy	9.2
Distance to nearest building	3.7
Soil cation exchange capacity	2.9
Annual precipitation	2.2
Soil coarse fragments	2.2
Surface water density	1.4

at the smaller (quadrant) scale, such that the product of these 2 outputs ($\psi * \theta$) represented occupancy probability at the smaller scale. We fitted our model as a function of environmental predictors at 2 different spatial resolutions (grid cells and quadrants). We accounted for imperfect detection of 3 types of data (acoustic with an MLE protocol [Britzke et al. 2002], acoustic with manual vetting, and capture data). Because both types of acoustic data used a secondary approach (i.e., MLE or manual vetting) to remove suspected false-positives before analysis, we did not consider false-positives in the occupancy model.

We modeled the occurrence state (z_{it}: presence/absence) of each grid cell and time period t as:

$$z_{it} \sim \text{Bernoulli}(\psi_{it}),$$

with

$$\text{logit}(\psi_{it}) = x'_i \beta + b_{year[t]} + \beta_{post} \times post_{it} + \beta_{connect} * S_{i,year[t]},$$

where x'_i was a matrix of site covariate values, β was a vector of covariate coefficients, $b_{year[t]}$ was the temporal random effect for year y, $post_{it}$ was an indicator for the post-volancy season (after 15 July), and β_{post} was the post-volancy effect coefficient. We assumed a first-order autoregressive [AR(1)] process, $[b_y] = AR(1)$ for years $y = 1, \cdots Y$, which is the same formulation as Udell et al. (2025). The linear predictor included the connectivity metric linking winter roost counts to the summer occupancy probability, similar to Udell et al. (2025), with as the winter-to-summer connectivity covariate for each grid cell and year, and as the covariate effect coefficient.

We used a multi-scale parameterization to represent the finer resolution of the nested quadrants (denoted q) within a grid cell i, where:

$$q_{qt} \sim \text{Bernoulli}(\theta_{qt} \times z_{it}),$$

and $\text{logit}(\theta_{qt}) = w' \alpha$ included covariates at the resolution of a quadrant q that explained local availability or occurrence. Here, θ_{qt} represented the probability of occurrence at the quadrant level, given occupancy at the grid-cell level (availability), and q_{qt} was the occupancy state at the quadrant level.

Observation submodels. For each observation "site-night" j, time period t, and location (grid cell i or quadrant q), we included an observation model with imperfect detection, given the latent true state (z_{it} or q_{qt}) and the detection probability p_{itj}, using the following general formulation: $y_{itj} \sim \text{Bernoulli}(p_{itj} \times z_{it})$ when data could only be reconciled at the grid cell, and when data could be reconciled at the quadrant. We estimated a different detection probability for each data type (MLE, manually vetted, capture) at each spatial scale (grid cell and quadrant), and we modeled p_{itj} as a function of daily covariates (day of year, minimum temperature, precipitation). For example, at the grid-cell scale we had:

$$y_{itj}^{\text{Grid-mle}} \sim \text{Bernoulli}(p_{itj}^{\text{Grid-mle}} \times z_{it}),$$
$$y_{itj}^{\text{Grid-vet}} \sim \text{Bernoulli}(p_{itj}^{\text{Grid-vet}} \times z_{it}),$$
$$y_{itj}^{\text{Grid-cap}} \sim \text{Bernoulli}(p_{itj}^{\text{Grid-cap}} \times z_{it}),$$

for acoustics using the MLE method ($y_{itj}^{\text{Grid-mle}}$), acoustics using manual vetting ($y_{itj}^{\text{Grid-vet}}$), and using captures ($y_{itj}^{\text{Grid-cap}}$). At the quadrant level, we had:

$$y_{qtj}^{\text{Quad-mle}} \sim \text{Bernoulli}(p_{qtj}^{\text{Quad-mle}} \times q_{qt}),$$

$$y_{qtj}^{\text{Quad-vet}} \sim \text{Bernoulli}(\text{p}_{\text{qtj}}^{\text{Grid-vet}} \times q_{qt}),$$
$$y_{qtj}^{\text{Quad-cap}} \sim \text{Bernoulli}(\text{p}_{\text{qtj}}^{\text{Grid-cap}} \times q_{qt}),$$

for acoustics using the MLE method ($y_{qtj}^{\text{Quad-mle}}$), acoustics using manual vetting ($y_{qtj}^{\text{Quad-vet}}$), and captures ($y_{qtj}^{\text{Quad-cap}}$). Thus, each of the response data types (3 methods, 2 spatial scales) had a separate detection function that we modeled as function of site- and observation-level covariates, also per Udell et al. (2025):

$$\text{logit}(\text{p}_{\text{itj}}^{x}) = \delta_0^x + \delta_1^x \times Doy_{itj} + \delta_2^x \times Doy_{itj}^{2} + \delta_3^x \times MinTemp_{itj} + \delta_4^x \times Precip_{itj},$$

with δ_0^x as the intercept for each response data type (x: Grid-mle, Grid-vet, Grid-cap, Quad-mle, Quad-vet, Quad-cap), and δ_1^x, δ_2^x, δ_3^x, δ_4^x as the covariate effects (coefficients) for each response data type.

We fitted the model in JAGS using R and the packages "R2jags" and "jagsUI" (Kellner 2024, Su and Yajima 2024). Specifically, we ran 3 Markov Chain Monte Carlo (MCMC) chains in parallel for 1000 adaptation iterations, followed by 15,000 total iterations (with 7500 used as burn-in). This procedure resulted in 22,500 samples from the joint posterior of each parameter. We evaluated models based on Area Under the Curve (AUC), which indicated classification accuracy of both presence and absence information.

We made predictions for occupancy probabilities for each grid cell and quadrant in the Northern Long-eared Bat range (U.S. Fish and Wildlife Service 2022a) in the contiguous United States. We report occupancy probability at the quadrant scale, which represents the product (ψ * θ) of occupancy at the grid-cell scale (ψ) and availability at the quadrant scale (θ). We made these predictions for each year in the pre-volancy season. Outputs provided predictions with uncertainty for each occupancy probability in each quadrant (which also includes each corresponding grid cell) and year. We calculated occupancy probability from 2017 to 2022 in each quadrant by averaging the occupancy probability over these years for each MCMC sample, which we then summarized as the mean and estimates of uncertainty (the 95% Bayesian credible interval; hereafter referred to as the 95% CI).

Results

Model inputs

Our dataset comprised 153,013 unique survey nights from 4177 unique grid cells. Stationary acoustic surveys included 73,161 survey nights with manual vetting and 52,792 survey nights with MLE calculations, while captures involved 27,060 survey nights (Fig. 2). Northern Long-eared Bats were detected in 9.4% of acoustic surveys and 11.8% of capture surveys. All data were available at the grid-cell scale, and 68.4% of data were available at quadrant resolution. We defined each "visit" as a unique survey night in a grid cell or quadrant in a year. Overall, sampled grid cells had a median of 7 total visits (interquartile range [IQR] = 3–21 visits), with 81.0% of these grid cells having at least 1 revisit. For grid cells with at least 1 revisit, 88.5% of revisits occurred on consecutive nights, with a median of 6 nights between the first and last visit (IQR = 2–20 nights).

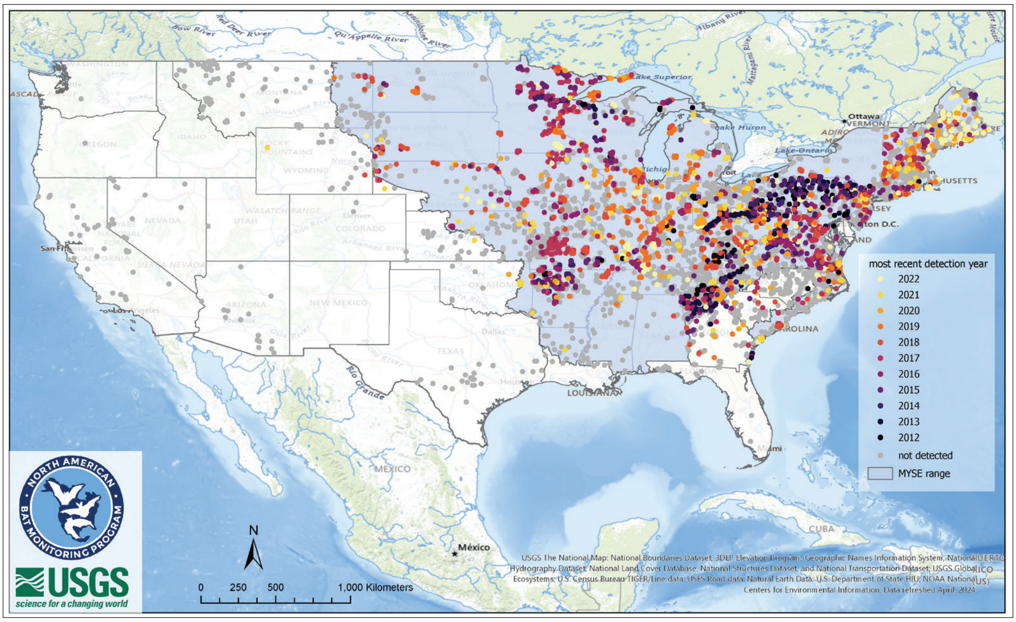
Model evaluation

We assessed MCMC chains visually and quantitatively. The standard "fuzzy caterpillar" trace plot indicated efficient sampling (Roy 2020) and R-hat values <1.1 also indicated that MCMC chain convergence was reached. We calculated AUC for each location and year with

MCMC samples of the latent state. The average unconditional (i.e., unconditional on the latent occupancy state) AUC was 0.637 (95% CI = 0.628–0.645) for presence/absence at the quadrant scale and 0.650 (0.641–0.657) at the grid-cell scale. These levels were considered acceptable in their predictive abilities (Hosmer et al. 2013). The average conditional AUC for predictions at the quadrant scale was 0.972 (0.969–0.975).

Occupancy and detection probability

Average detection probability was 0.53 (95% CI = 0.53–0.54) for MLE acoustic surveys, 0.034 (0.032–0.037) for vetted acoustic surveys, and 0.22 (0.22–0.25) for capture surveys. The average occupancy probability for our predictions at the quadrant scale was 0.38 (0.35–0.41; Fig. 3). At the grid-cell scale, the presence of karst, the post-volancy indicator, the roost-suitability metric, and the connectivity metric had positive effects on occupancy probability (Fig. 4A). At the quadrant scale, the proportion of wetlands and the roost-suitability metric had a positive influence on availability, i.e., the probability of local occupancy given presence at the grid-cell scale (Fig. 4A). Random intercepts for each year indicated that occupancy probability was higher, on average, in earlier years (Fig. 4B).



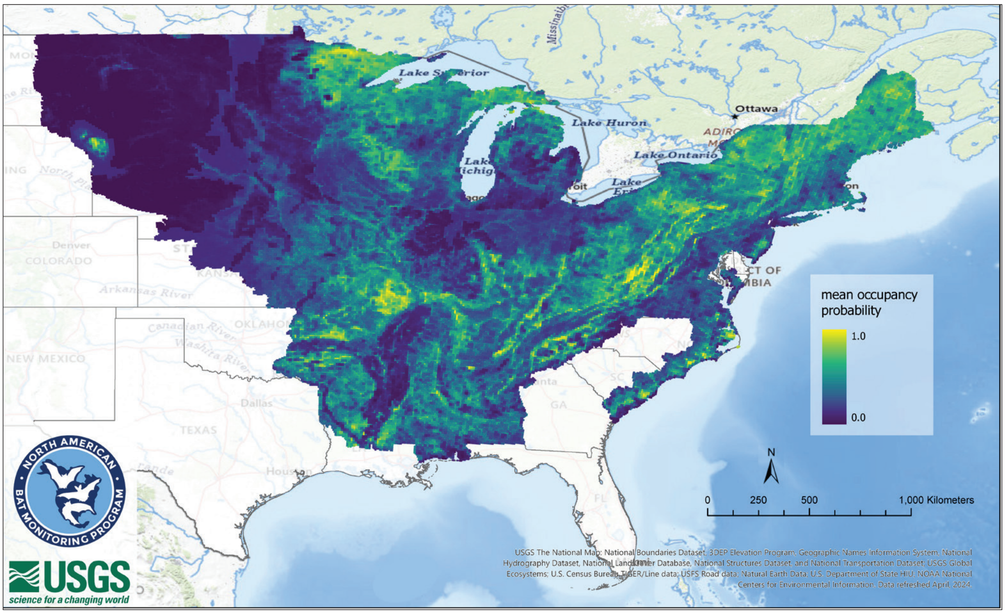
USGS The National Map: National Boundaries Dataset, 3DEP Elevation Program, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; USGS Global Ecosystems; U.S. Census Bureau TIGER/Line data; USFS Road data; Natural Earth Data; U.S. Department of State HIU; NOAA National Centers for Environmental Information. Data refreshed April, 2024.

Figure 2. Sampling effort and coverage for stationary acoustic and capture records included as model input for *Myotis septentrionalis* (Northern Long-eared Bat), from 2012 to 2022. Points represent centroids of grid cells. Grid cells with survey effort, but no detections of Northern Long-eared Bats, are shown in gray. Capture surveys include all capture events for any bat species. Stationary acoustic records include surveys for which the Northern Long-eared Bat was included in the classifier. Specifically, acoustic records include manually vetted detections and auto ID detections retained after maximum likelihood estimator (MLE) processing. For grid cells with detections of the Northern Long-eared Bat, color represents the most recent detection year. For overlapping points, more recent detections appear on top of less recent detections, and detections are shown on top of non-detections. Periwinkle shaded area within the polygon indicates the target species range (U.S. Fish and Wildlife Service 2022a) in the contiguous United States.

For acoustic surveys at both scales, precipitation had a negative influence on detection probability, while minimum temperature had a positive effect. Conversely, for capture surveys, precipitation had a positive effect on detection probability, and minimum temperature had a negative effect. We note that here, weather variables represented daily totals (for precipitation) and daily minima (for temperature) at the centroid of a grid cell or quadrant, not necessarily the conditions at a specific site or within the duration of the survey. For all survey types, day of year had a negative effect on detection probability, while quadratic day of year was positive for acoustic surveys and negative for capture surveys (see Supplemental Table S2, available online at https://eaglehill.us/urnaonline/suppl-files/nabr-018-Wray-s1.pdf).

Discussion

Overall, we found that despite the low detection probability associated with Northern Long-eared Bats, the expansive amount of data available enabled prediction of occupancy probability at a multi-scale resolution across their range within the contiguous United States. As Northern Long-eared Bats, like many other bats, are mobile and can use multiple roost trees in a season (e.g., Silvis et al. 2015, Thalken and Lacki 2018), incorporating multiple data types in an occupancy modeling framework can yield insights on habitat characteristics and landscape features beyond point locations for roosts. Since maternity colonies of Northern Long-eared Bats often consist of complex networks (Gorman et al. 2023, Johnson et al. 2012), predictive modeling may also help inform estimates of habitat use by these bats in areas that have not been or cannot be surveyed.



USGS The National Map: National Boundaries Dataset, 3DEP Elevation Program, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; USGS Global Ecosystems; U.S. Census Bureau TIGER/Line data; USFS Road data; Natural Earth Data; U.S. Department of State HIU; NOAA National Centers for Environmental Information. Data refreshed April, 2024.

Figure 3. Summer occupancy probabilities for *Myotis septentrionalis* (Northern Long-eared Bat), predicted at the quadrant scale and averaged over the years 2017–2022. Results are clipped to the species range (U.S. Fish and Wildlife Service 2022a) in the contiguous United States. Color represents mean occupancy probability. The product of occupancy at the larger (grid-cell) scale (ψ) and availability (local occupancy given presence, θ) represents occupancy probability at the smaller (quadrant) scale.

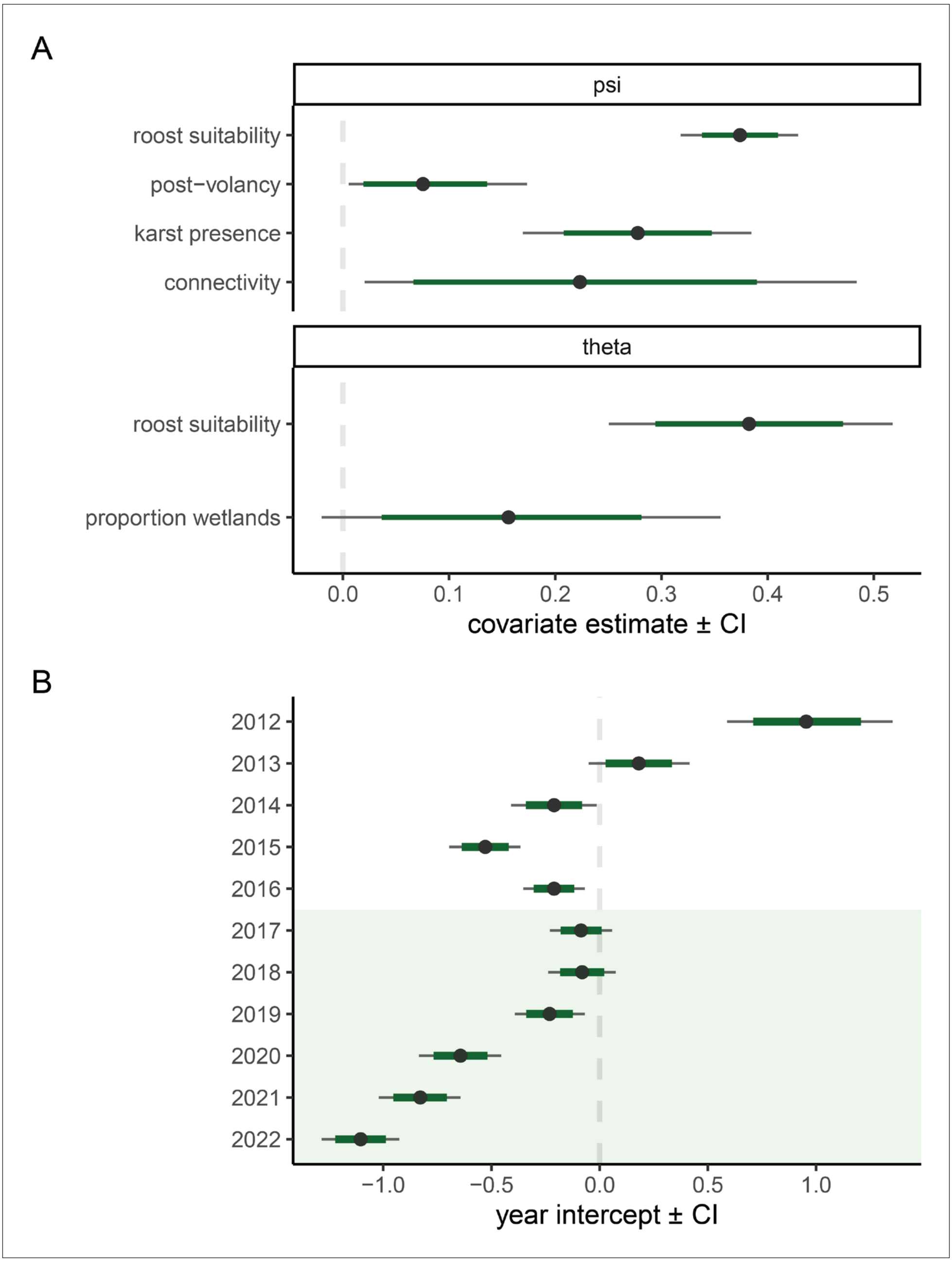


Figure 4. Summer occupancy model covariates for *Myotis septentrionalis* (Northern Long-eared Bat), from 2012 to 2022. A) Estimates for predictors of occupancy (ψ) at the grid-cell scale and availability (local occupancy given presence, θ) at the quadrant scale. B) Year intercepts with 95% and 80% credible intervals (CI). The light green box highlights years for which occupancy probabilities were predicted at the quadrant scale and averaged, as shown in Figure 3. For A and B, points represent mean estimates, thinner black lines represent 95% credible intervals, and thicker green lines represent 80% credible intervals.

While autoclassification remains imperfect, by incorporating manually vetted stationary acoustic records, as well as capture data, this study provides updated, data-driven predictions of where Northern Long-eared Bats are likely to be found. False-positive occupancy models, which account for potential misidentifications, can be useful for improving the accuracy of estimates from acoustic surveys (e.g., Rojas et al. 2019), but in a Bayesian framework, these models are computationally intensive. Using MLE metrics for acoustic surveys without manual vetting may help reduce the influence of unlikely detections, although this treatment can also result in the loss of some true detections and could be improved by using other sampling designs or detection models (Irvine et al. 2022, Specht et al. 2017). While we limited our predictions to the currently described range of the Northern Long-eared Bat in the contiguous United States, we note that our data inputs included several detection records from outside the published range (U.S. Fish and Wildlife Service 2022a). For example, several stationary acoustic detections were reported from western Wyoming, which included records without manual vetting, but that did pass the MLE threshold for inclusion. In several other areas, Northern Long-eared Bats have been identified by auto ID, but without validation via captures. Further surveys of these areas or retrospective manual vetting could help improve the quality of data inputs for these types of models and our understanding of the current range of this species.

The covariates used in the model were statistically meaningful as predictors and biologically plausible, given the ecology of this species and findings from previous occupancy models based on the NABat database (Udell et al. 2022a, b). For example, the roost-suitability metric, which was primarily driven by canopy cover, had a strong positive effect at both spatial scales, which is consistent with habitat use and roosting preferences of Northern Long-eared Bats (e.g., Broders et al. 2006, Foster and Kurta 1999, Lacki et al. 2009). Studies on other types of animals have used predicted habitat-suitability layers from presence-background models as inputs for occupancy models (e.g., da Silva Neto et al. 2020), although these approaches have not been frequently used for bats. Future use of habitat-suitability layers as occupancy modeling covariates may help expedite computationally intensive modeling efforts by consolidating important predictor covariates. Rather than perform intensive model selection or comparison, we selected other covariates *a priori* based on the ecology of Northern Long-eared Bats. While not incorporated into the roost-suitability metric, wetlands and riparian areas can provide suitable habitat for this species in certain areas (Foster and Kurta 1999; Gorman et al. 2022; Jordan 2020; Udell et al. 2022a, b). Similarly, by using a seasonal connectivity metric, our model accounts for the presence of nearby hibernacula that may influence Northern Long-eared Bat summer distributions (Hoff et al. 2024). Expansion of model comparisons, or the incorporation of different sets of covariates, could yield improved predictive power. Indeed, while our conditional AUC scores (the probability of presence at the quadrant scale, given presence at the grid-cell scale) were high, the unconditional scores (the probability of occupancy without considering latent random effects) were considered acceptable, but could be improved with additional data.

Although our model treats separate stationary acoustic surveys (i.e., any survey with a unique combination of location, date, project, and equipment) as separate observers, we did not include specific parameters to account for potential heterogeneity between observers. Factors such as equipment type—like models of acoustic detectors, microphone types, software versions, and the condition of recording equipment—may affect detection probability within specific years, and advancements in autoclassification technology could also influence detection probabilities over time. Though we did not account for these potential effects, our results showed that later years generally had lower occupancy probabilities, which is consistent with other studies that described declining populations of Northern Long-eared Bats (e.g., Cheng et al. 2021; Udell et al. 2022a, b; White et al. 2022). Since our primary focus was estimating the recent (2017–2022) distribution of Northern Long-eared Bats, we do not over-interpret this declining trend. While previous work has documented population declines, the observed year effects in this study could be influenced by changes in survey effort associated with the geographic spread of white-nose syndrome. As such, follow-up studies, which may incorporate more nuanced parameterization of spatiotemporal heterogeneity in observation quality and/or observation effort (e.g., Kery et al. 2010), may be warranted for updating estimates on population trends of Northern Long-eared Bats.

Our model (Fig. 3) predicted higher occupancy probability in areas where Northern Long-eared Bats have been persisting, including North Carolina (Jordan 2020), central Pennsylvania (Lewis et al. 2022), and some coastal regions of New England (Hoff et al. 2024). Though some areas with high predicted occupancy probability, such as central New York state, were not strongly represented by available data, our results suggest that additional survey effort in these regions is warranted and could provide further ground-truthing for the chosen modeling approach. Our study also indicated a patch of high occupancy probability in northeastern Wyoming and western South Dakota, a region that includes Black Hills National Forest and the Bear Lodge Mountains. Northern Long-eared Bats have been captured in this patch and nearby locations (Alston et al. 2019, Cryan et al. 2000). The aforementioned patch appears somewhat isolated, which could reflect a lack of survey data in areas between this patch and the other parts of the species' range with higher occupancy probability. Although some portions of the Northern Long-eared Bat range remain underrepresented in terms of data availability, extensive sampling efforts covered a large geographic scale and included a broad suite of habitat conditions in our study. While it is possible that unmeasured climate or landcover variables could be unique among unsampled grid cells, the ranges of values for the covariates included in our model did not differ substantially between sampled and unsampled grid cells where predictions were made. Our scope of inference was confined to the continental United States, though the distribution of the Northern Long-eared Bat continues northward and westward into Canada, and thus, additional areas of high occupancy may not be captured.

Occupancy modeling is not without its caveats, and like all models, the quality of model outputs is inherently linked to the quality of data inputs. Acoustic monitoring is imperfect, even for manually vetted records. Manually vetted records may be biased if, for example, vetters are highly conservative in downgrading auto IDs of Northern Long-eared Bat to "*Myotis* spp." or other ambiguous classification, which may also account for the low average detection probability in this study. Similarly, auto IDs without manual vetting may retain false positives due to ambiguity in echolocation calls. By applying an MLE threshold, we attempted to reduce the potential influence of false positives. However, this data filtering also resulted in loss of some data that could not be processed through MLE due to a lack of appropriate performance tables. Future changes to the NABat database, such as allowing for the inclusion of automatically generated MLE scores from other classification software, may provide additional options for data inclusion in modeling efforts. Incorporating additional data, especially in areas with high predicted occupancy probability without existing surveys, could further improve the accuracy of future predictions.

Ground-truthing model estimates could further validate our results, highlighting the utility of the NABat database and the improved ability to test model predictions following the incorporation of additional data. We note that our multi-scale approach correctly accounts for spatial autocorrelation at the grid-cell scale when modeling the quadrant scale. However, given common computational limitations in occupancy modeling, we did not attempt to accommodate additional autocorrelation beyond this, which, if present, could lead to over-precise parameter estimates, but is unlikely to result in bias. The basic assumptions of occupancy modeling for mobile species (e.g., MacKenzie et al. 2006) were reasonable for our study design and system for the following reasons: the interpretation of occupancy as use of a grid-cell quadrant by at least 1 individual, the assumption of closure at the species level (i.e., the occupancy state as defined above does not change), and the short distances (with respect to grid cell quadrants) of the general within-season movements of the Northern Long-eared Bat.

On a global scale, narrow-space foraging, low-wing aspect ratio bat species (which often includes species reliant on forest interior habitat) face many threats (Jones et al. 2003, Safi and Kerth 2004). As these bats can be difficult to capture with standard techniques (e.g., Tanshi et al. 2022) or challenging to detect with acoustic methods (Froidevaux et al. 2014, Patriquin et al. 2003), future occupancy modeling for other forest-associated species may require finding creative solutions for coping with low detection probabilities. Despite the challenges associated with predicting occupancy for rare, cryptic species, there is a need to quantify the distribution of these species beyond direct observations. Our analysis highlights the utility of centralized databases that house multiple data types, which can be used to improve data-driven estimates of where species are likely to occur.

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Data availability

Data are available by request via the NABat database. This study references data requests number 290 (capture data) and 291 (stationary acoustic data), created on 2 April 2024, which include all Northern Long-eared Bat records from all years. JAGS script, model outputs, and additional raw data processing details are available on ScienceBase: https://doi.org/10.5066/P1BE5QTK. Model outputs are available in supplementary materials.

Non-endorsement of commercial products and services

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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