

Comparing occupancy and activity metrics for assessing temporal trends in vulnerable bat populations

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ABSTRACT

Appropriately monitoring vulnerable species is essential for resource management decision-making. We used two different metrics (occupancy and acoustic activity) to evaluate population trends of North American bats susceptible to a fungal disease and compared the outcomes of these two analyses. Our dataset consisted of passive acoustic survey data collected at nine U.S. national parks in the Great Lakes region between 2016 and 2020. Our focal species were little brown bat (*Myotis lucifugus*), northern long-eared bat (*Myotis septentrionalis*), tricolored bat (*Perimyotis subflavus*), and big brown bat (*Eptesicus fuscus*). Combining acoustic detection data with site-specific and environmental covariates, we developed park- and species-specific models of occupancy (use) and acoustic activity. For little brown, northern long-eared, and tricolored bats, probability of use declined 20 % and activity declined 66 %, on average. For big brown bat, probability of use decreased 9 % and activity increased 17 %. Our results showed that use of space and level of activity were not predicted by the same covariates but were positively related. We also found probability of use could remain high while activity decreased to relatively low levels. Although we observed precipitous declines in activity rates of three species, they were still using a high proportion of the landscape. We conclude that analyzing activity provides different but complementary information to analyzing species' use of space. The two metrics vary on different temporal and spatial scales and have different biases. Appropriate choice of which parameter to analyze is crucial, as different parameters may lead to different ecological conclusions, thus affecting how management decisions are made and how species conservation and recovery efforts are implemented.

1. Introduction

Effective management of vulnerable wildlife species requires understanding which populations are at risk and to what degree. Consistent monitoring across time and space provides data to evaluate species' status and trends and identify sensitive populations (Lindenmayer et al., 2022). However, choices about study design and which variables to measure can impact inferences, which in turn affect how species

management and recovery efforts are implemented (Yoccoz et al., 2001). Here, we evaluate the implications for monitoring threatened bat populations. Globally, bats face many threats including habitat loss, persecution, and wind energy development (Frick et al., 2020). In North America, bats are additionally threatened by white-nose syndrome (WNS), a disease devastating to hibernating bat populations (Hoyt et al., 2021).

WNS is caused by a fungus, *Pseudogymnoascus destructans*, that

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infects bats during their winter hibernation (Blebert et al., 2009; Gargas et al., 2009). First recorded in North America in 2006, the disease has since spread across much of the continent (White-Nose Syndrome Response Team, 2023). At least partially due to WNS impacts, several bat species are listed as endangered or threatened in the U.S. and Canada (Government of Canada, 2022; USFWS, 2022a, 2022b). Significant WNS-related population declines have been documented for the little brown bat (*Myotis lucifugus*), northern long-eared bat (*Myotis septentrionalis*), and tricolored bat (*Perimyotis subflavus*) (Nocera et al., 2019; O'Keefe et al., 2019; Cheng et al., 2021). However, the status of big brown bats (*Eptesicus fuscus*) after the arrival of WNS has been more variable. Declining (Cheng et al., 2021), increasing (Kurta and Smith, 2020), and stable (Huebschman, 2019) trends have all been documented. Big brown bats have different hibernation behaviors than other species, for example hibernating in buildings and often roosting alone rather than in a cluster (Whitaker and Gummer, 2000). These behaviors, coupled with unique physiological and behavioral responses to the WNS infection (Frank et al., 2014; Moore et al., 2018), could explain big brown bat persistence in areas where other hibernating species have declined precipitously.

Prompted by the growing threat of WNS and other stressors on bat populations, the U.S. National Park Service (NPS) initiated regional-scale acoustic monitoring programs (e.g., Rodriguez et al., 2019; Goodwin, 2020), aiming to document species distributions and trends over time and fill gaps in knowledge regarding bats in national parks (Rodhouse et al., 2016). Acoustic monitoring is an efficient, cost-effective, noninvasive methodology that passively records bats' echolocation calls with automated sensors (Gibb et al., 2019). Standardized long-term, broad-scale acoustic monitoring efforts such as these NPS programs can inform status and trends assessments for vulnerable bat species, thus guiding conservation and management actions. An important consideration when planning these monitoring programs is how the resulting data will be analyzed (for example, looking at species' presence, spatial or temporal distribution, relative abundance, or trends over time), as this will impact study design and level of effort required.

Two common approaches to understanding drivers of change in species populations are modeling species' occurrence or species' abundance (MacKenzie et al., 2018). Using occupancy modeling methods, we can estimate the probability that a species is occupying or using an area, while accounting for imperfect detection (MacKenzie et al., 2003). Similarly, we can use various types of abundance models to estimate population size. For bats, acoustic activity can be used as an index of abundance (Revilla-Martín et al., 2021; Whiting et al., 2022). Bat acoustic activity is typically measured as a count of echolocation call sequences per unit of time, allowing comparisons of relative activity across species, locations, or time (e.g., Bombaci et al., 2021).

Assessing occurrence or abundance can provide insight into the status of imperiled species. Most studies of bats investigate one metric or the other, not both; however determining which measure is most appropriate can be difficult. The relationship between abundance and occurrence is typically positive, though importantly, it can be influenced by species' behavior, sampling scale, or other factors (Gaston et al., 2000; Steenweg et al., 2018). Species' use of space and species' abundance vary over different spatial and temporal scales (Gaston et al., 2000; Latham et al., 2014). In highly mobile species such as bats, relatively stable occurrence rates can occur alongside rapidly changing activity rates (Law et al., 2020; Nocera et al., 2020). Furthermore, although factors such as forest structure and proximity to water can influence both bats' use of space and their activity levels (Blakey et al., 2019; Gorman et al., 2022), the effects may differ (Dibner et al., 2017).

For this study, our first objective was to model temporal trends in both the probability of a species using an area and a species' acoustic activity level over a five-year period for bats affected by WNS. Our second objective was to assess the importance of covariates such as land cover, weather, and time of year. Finally, our third objective was to characterize the relationship between bat use and bat activity, compare

the outcomes of modeling these two different parameters, and assess the suitability of each parameter for different management situations. Our study evaluates four species (little brown bat, northern long-eared bat, tricolored bat, big brown bat) and offers a uniquely broad, regional-scale perspective.

2. Methods

2.1. Study area

The NPS Great Lakes Inventory and Monitoring Network coordinates bat acoustic monitoring at nine U.S. national parks: Apostle Islands National Lakeshore (APIS), Grand Portage National Monument (GRPO), Indiana Dunes National Park (INDU), Isle Royale National Park (ISRO), Mississippi National River and Recreation Area (MISS), Pictured Rocks National Lakeshore (PIRO), Saint Croix National Scenic Riverway (SACN), Sleeping Bear Dunes National Lakeshore (SLBE), and Voyageurs National Park (VOYA; Fig. 1). The nine parks total over 455,000 ha and contain a variety of forest types including savanna, deciduous hardwood, mixed deciduous-coniferous, boreal conifer, and floodplain. Emergent and shrub wetlands, lakes, and ponds are also common. Two parks are located along major river corridors (MISS, SACN). Five parks have extensive shoreline along Lake Superior or Lake Michigan (APIS, INDU, ISRO, PIRO, SLBE). Two parks are within highly developed urban areas (INDU, MISS) while the remaining parks are more remote; five contain federally designated or proposed wilderness (APIS, ISRO, PIRO, SLBE, VOYA). Timing of WNS arrival varies by park; the disease was detected earlier in the eastern and southern parts of our study area (White-Nose Syndrome Response Team, 2023).

2.2. Acoustic data collection and processing

Study design and field methods are detailed in Goodwin (2020). To summarize, we selected sampling locations from a grid of 1-km² cells overlaid on each park, using generalized random-tessellation stratification (Stevens and Olsen, 2004). Within each selected cell (18–35 per park), we identified one sampling site based on suitable bat habitat and accessibility. We conducted passive acoustic surveys at each site once per year, averaging nine nights per deployment (range: 1–30). Surveys occurred between 1 June and 15 August, in 2016–2020.

We used three acoustic detector models: Song Meter SM3BAT and SM4BAT-FS detectors with SMM-U1 omnidirectional microphones (Wildlife Acoustics Inc., Maynard, MA, USA) and D500x detectors with D500x microphones (Pettersson Elektronik AB, Uppsala, Sweden). Wildlife Acoustics microphones were fitted with foam windscreens. Pettersson microphones were fitted with directional horns and placed inside tubes for weatherproofing. We used sampling rates of 256 kHz for the SM3BAT and SM4BAT and 500 kHz for the D500x. All detectors recorded in full spectrum format. One park (PIRO) used only D500x detectors; all other parks used a combination of SM3BAT and SM4BAT detectors. Though we expect recording results to vary between detector brands (Barr, 2019) our main objective was to assess trends within each park rather than across parks, and detector brand remained consistent within each park. We oriented microphones towards open air space and elevated them off the ground at a mean height of 2.8 m (range: 1.5–5.7 m) (Appendix Table A1).

We processed acoustic files using Kaleidoscope Pro software (Version 5.4.2, Wildlife Acoustics Inc., Maynard, MA, USA) to filter out noise and classify recordings to species. To ensure comparability, we processed all files using identical software settings (Goodwin and Gillam, 2021). We used Bats of North America Classifier Version 5.4.0 with sensitivity set to –1 (“Liberal”). We used default signal detection parameters (frequency 8–120 kHz, pulse length 2–500 ms, and 500 ms maximum inter-syllable gap) but increased the required minimum number of pulses to five, instead of the default of two, in order to avoid classification of poor quality or truncated recordings. We did not manually vet species

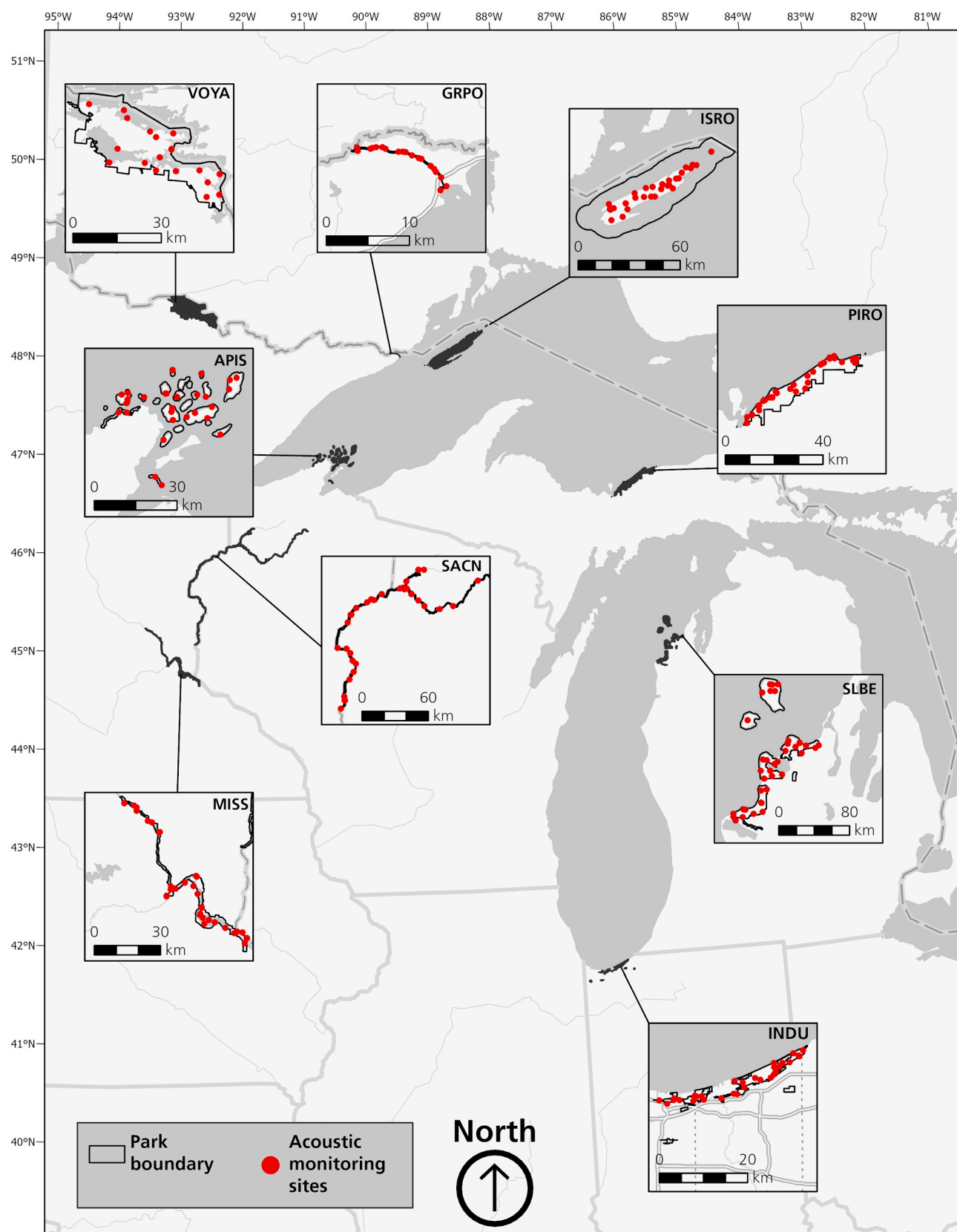


Fig. 1. Bat acoustic monitoring was conducted at nine U.S. national parks in the western Great Lakes region. Parks include Apostle Islands National Lakeshore (APIS), Grand Portage National Monument (GRPO), Indiana Dunes National Park (INDU), Isle Royale National Park (ISRO), Mississippi National River and Recreation Area (MISS), Pictured Rocks National Lakeshore (PIRO), Saint Croix National Scenic Riverway (SACN), Sleeping Bear Dunes National Lakeshore (SLBE), and Voyageurs National Park (VOYA).

classifications due to the large size of our dataset. While classification errors do occur, our use of the software ensures consistency and objectivity (Fraser et al., 2020).

During classification, we considered all bat species whose documented ranges overlap or approach each park's boundary (Kurta, 2017). Seven species found throughout the Great Lakes region were included for all parks: big brown bat, eastern red bat (*Lasiurus borealis*), hoary bat (*Lasiurus cinereus*), silver-haired bat (*Lasionycteris noctivagans*), little brown bat, northern long-eared bat, and tricolored bat. For the more southerly parks, we also included evening bat (*Nycticeius humeralis*; INDU, MISS, SACN) and Indiana bat (*Myotis sodalis*; INDU, SLBE).

From Kaleidoscope Pro outputs, we obtained nightly counts of files with species-level classifications and nightly presence *p*-values for each species at each site. Kaleidoscope Pro uses a maximum-likelihood estimation method based on the likelihood-ratio test of species absence developed by Britzke et al. (2002), such that a *p*-value near zero suggests probable presence (Wildlife Acoustics, Inc., 2021).

2.3. Occupancy modeling

We used a dynamic occupancy model (MacKenzie et al., 2003) to estimate occupancy and detection parameters over multiple years, modeling each park-species combination separately. We performed all occupancy modeling in R (Version 4.1.2; R Core Team, 2021) using the *unmarked* package (Version 1.1.1; Fiske and Chandler, 2011). Since our 1-km² sampling units are smaller than the foraging ranges of our focal species, we cannot assume units are closed to changes in occupancy during sampling; therefore we interpret the occupancy parameter as the probability of a species using the area (MacKenzie et al., 2018).

We considered a positive detection to have occurred at the site-night level when a species had ≥ 1 call file and a presence *p*-value of < 0.05 , based on the Kaleidoscope Pro results. This threshold is equivalent to U.S. Fish and Wildlife Service (USFWS) guidelines (USFWS, 2023). Park-species combinations with positive detections on $< 5\%$ of detector-nights were excluded from further analyses due to insufficient data (Appendix Fig. A1). Due to variability in total number of recording nights per deployment (range: 1–30, median: 9) and resulting model instability, we used only 4 nights per deployment. We excluded all deployments with < 4 nights (31 out of 995 deployments). For deployments with ≥ 4 nights, we randomly selected 4 nights, mitigating potential temporal autocorrelation.

We considered microphone height, clutter distance, weather conditions, days after leaf-out, and survey year as potential covariates affecting detection probability. For each sample site, we calculated mean microphone height and mean clutter distance across all years of surveys, yielding site-specific detection covariates (Appendix Table A1). At the time of detector deployment, we recorded microphone height off the ground and distance from the microphone to the nearest clutter. Clutter includes landscape features that reflect or distort sound, thus reducing recording quality; at our sites this includes vegetation, buildings, and water. Water also attracts bats, increasing the possibility of multiple overlapping echolocation sequences in the same recording, which makes files less identifiable. Clutter distance was recorded using eight distance classes: < 5 m, 5 m, 10 m, 20 m, 50 m, 75 m, 100 m, or > 100 m. For analysis purposes, we converted these distance classes to numerical values, using 2.5 m for the < 5 m class and 125 m for the > 100 m class. We included survey year as a covariate to account for the increasing influence of WNS in our study area over time (Mallinger et al., 2023).

Previous work demonstrates bat activity varies with temperature, humidity, wind, and precipitation (Squires et al., 2021; Andreozzi et al., 2024). In addition, weather conditions affect the atmospheric attenuation of sound, particularly for high-frequency sounds (Goerlitz, 2018). We obtained weather data from automated airport weather stations (Iowa State University, 2021), using the station nearest to each park with the most complete summer data. Weather stations were located an

average of 39 km (range: 2–93 km) from sampling sites (Appendix Table A1). We summarized observations over each 24-hour nightly period (12:00 pm to 11:59 am) by calculating minimum air temperature, mean percent relative humidity, mean wind speed, and maximum precipitation. We used these values as date-specific detection covariates, corresponding to the night each audio file was recorded.

Because the parks are located across a range of latitudes, we used days after spring leaf-out as a measure of seasonal phenology rather than calendar date. We obtained leaf-out dates from the Extended Spring Index of First Leaf raster dataset, which predicts local timing of leaf-out based on historical observations of certain shrub species (USA National Phenology Network, 2020). We identified the first leaf date for each sample site in each year, then calculated the number of days after the first leaf date corresponding to each sampling date. Days after first leaf-out were used as a date-specific detection covariate.

We considered elevation, canopy height, and land cover as potential site-specific covariates affecting the probability of a species using an area. We used LiDAR data (2-m resolution) to determine elevation at each sample site and mean canopy height within a 1-km buffer around each site (U.S. Geological Survey, 2021; Tables S1, S2). We generated canopy height using the *lidR* package in R (Roussel et al., 2020). We obtained land cover classification data from the 30-m resolution National Landcover Dataset (Dewitz, 2019). This dataset includes 16 land cover classes, which we reassigned to four broader classes: forest, developed, open land, and open water (Appendix Table A3). We calculated the percentage of each class within a 1-km buffer around each site (Appendix Table A2). The 1-km buffer roughly approximates the mean foraging home range sizes of our species of interest, which range from 102 to 622 ha (Wilkinson and Barclay, 1997; Coleman et al., 2014a; Divoll et al., 2022; Thorne et al., 2021; Cable and Wilcox, 2024). All covariates except survey year were scaled prior to fitting models, by subtracting the mean and dividing by the standard deviation.

We used a two-stage occupancy modeling procedure (MacKenzie et al., 2018). First, for each park-species combination, we fit 19 candidate detection models (Appendix Table A4). Except for our completely null model, each candidate model included a global model for initial occupancy, while colonization and extinction were held constant. The completely null model set all four parameters (initial occupancy, colonization, extinction, and detection) as constant. Using Akaike's Information Criterion (AIC), we identified the top detection model by selecting the model with the lowest AIC value (discarding models that did not converge). However, if there was a nested model with fewer covariates within the group of models with substantial support ($\Delta AIC < 2$; Burnham and Anderson, 2002), we selected that simpler model. Second, we fit 14 candidate occupancy models (Appendix Table A5), using the previously-identified most important detection parameters for each park-species combination. Again, except for our completely null model, we held colonization and extinction constant. We identified the top occupancy model using the same criteria described above. We tested the addition of a survey year covariate on the colonization and extinction parameters, but model ranking outcomes were not meaningfully different, therefore we retained the constant formula for both the colonization and extinction parameters. To assess goodness-of-fit for final models, we used parametric bootstrapping with a chi-square fit statistic (Fiske and Chandler, 2019). Finally, we derived estimates of the occupancy parameter for years after the initial year via the "smoothed" function in the *unmarked* package, and computed associated standard errors through bootstrapping (Kéry and Chandler, 2016).

2.4. Activity modeling

We used generalized linear mixed models to estimate acoustic activity levels over time, again modeling each park-species combination separately. We used the R packages *glmmTMB* to fit models (Brooks et al., 2017) and *MuMIn* to run model selection (Barton, 2020).

We compared a set of 13 candidate models (Appendix Table A6),

using the count of audio files classified to the species of interest as the response variable. We specified a negative binomial distribution due to overdispersion in the count data. All candidate models included survey year as a fixed effect plus two random effects: number of recording nights in the deployment (all nights of data were used) and site identifier. Each model except the null model included additional fixed effects testing the importance of elevation, canopy height, and land cover, which were derived as described above. We identified the top model using the same criteria as for occupancy modeling (most parsimonious model from among those that converged and had a $\Delta AIC < 2$).

2.5. Activity-occupancy comparison

To evaluate the relationship between acoustic activity and use of space, we plotted model-estimated probability of use for each species-park-year combination against the corresponding model-estimated relative activity level. We calculated relative activity level as model-estimated activity (call files per detector-night) for a particular species-park-year combination divided by the maximum estimated activity of any species-park-year combination.

3. Results

We surveyed during 3–5 summers at each park between 2016 and 2020. Per park, we completed an average of 111 deployments (range: 77–147) and 286 recording nights (range: 182–348). In total, we collected 1,234,686 audio files identifiable to the species level (mean: 137,187 per park; range: 16,973–365,079).

The yearly mean proportion of detector-nights with a positive detection ranged from 0.0 for tricolored bat in 2020 to 0.69 for little brown bat in 2016 (Appendix Table A7). Little brown and big brown bats had more positive detections than northern long-eared and tricolored bats. Fourteen park-species combinations had positive detections on $< 5\%$ of detector-nights and were excluded from further analysis

(Appendix Fig. A1). The remaining 22 park-species combinations had sufficient data for analysis: all nine parks for little brown bat, six parks for big brown bat, five parks for northern long-eared bat, and two parks for tricolored bat.

3.1. Occupancy modeling

Probabilities of use and trends in probabilities varied by species and by park (Fig. 2). Model-predicted probability of use for little brown bat ranged from 0.22 to 1.0; for northern long-eared bat from 0.12 to 0.84; for tricolored bat from 0.04 to 0.78; and for big brown bat from 0.32 to 1.0. For little brown bat, probability of use decreased at eight out of nine parks, dropping by 11–56 % from the first year of surveys to the last. At the ninth park (INDU), probability of use increased by 65 %. For northern long-eared bat, probability of use declined by 35–78 % at three parks (GRPO, MISS, VOYA) and increased 6–34 % at two parks (APIS, ISRO). Probability of use for tricolored bats at SACN declined by 87 %, while at MISS it declined by 6 %. Big brown bat probability of use was stable ($< 5\%$ change) at five out of six parks (INDU, ISRO, MISS, SACN, and SLBE) but decreased by 51 % at PIRO.

In the best supported occupancy models, the covariate that was most frequently related to detection probability was survey year, which was included in 10 of 22 models (Table 1; Appendix Tables A8, A10). Other important predictors included clutter distance, microphone height, and days after leaf-out. The covariates that were most frequently related to initial occupancy probability were percent cover of open land, percent cover of open water, and elevation (Table 1; Appendix Tables A8, A11). Six of the best supported final models did not include any covariates for the detection parameter, and five did not include any covariates for the initial occupancy parameter (Table 1; Appendix Table A8).

3.2. Activity modeling

Activity levels and trends varied by species and park (Fig. 2). Model-

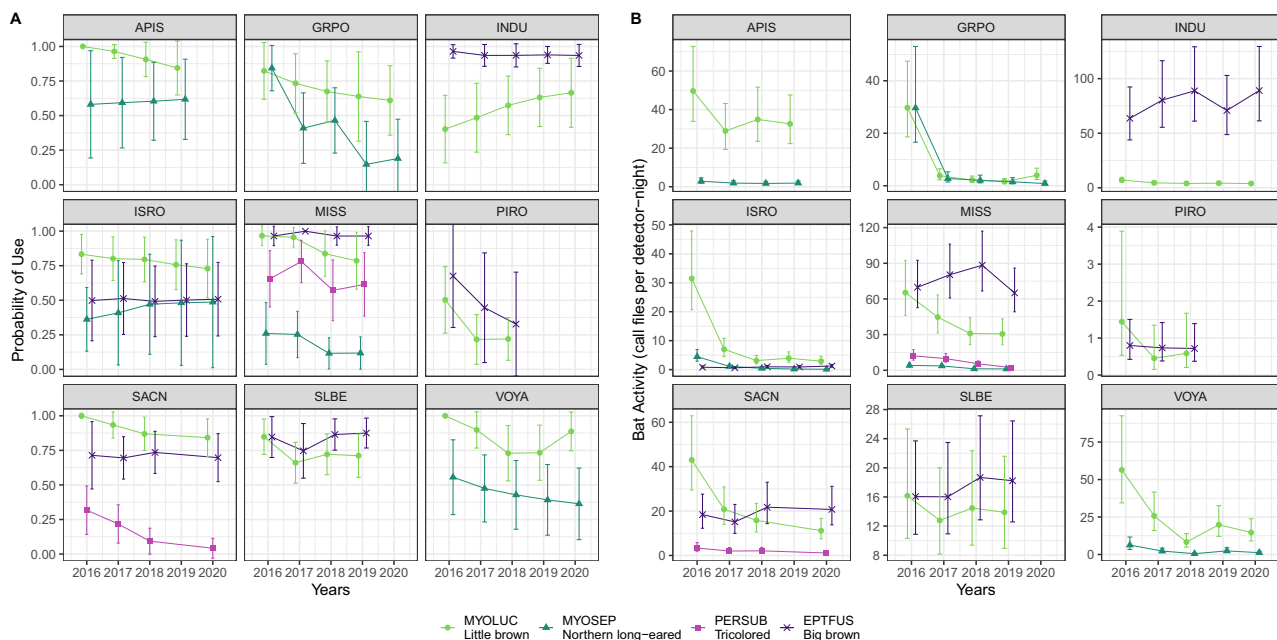


Fig. 2. A) Model-predicted probability of use and B) Model-predicted acoustic activity by year for little brown bat (MYOLUC, *Myotis lucifugus*, green circle), northern long-eared bat (MYOSEP, *Myotis septentrionalis*, blue triangle), tricolored bat (PERSUB, *Perimyotis subflavus*, pink square), and big brown bat (EPTFUS, *Eptesicus fuscus*, purple cross) at nine U.S. national parks, 2016–2020. Parks include Apostle Islands National Lakeshore (APIS), Grand Portage National Monument (GRPO), Indiana Dunes National Park (INDU), Isle Royale National Park (ISRO), Mississippi National River and Recreation Area (MISS), Pictured Rocks National Lakeshore (PIRO), Saint Croix National Scenic Riverway (SACN), Sleeping Bear Dunes National Lakeshore (SLBE), and Voyageurs National Park (VOYA). For A) points indicate the probability of sampled sites being used by the species; bars indicate standard errors. For B) points indicate mean bat activity in call files per detector-night; bars indicate 95 % confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Best-supported occupancy model for each park and species. Our two-stage model selection process consisted of first testing 19 candidate detection models, then incorporating the best-supported detection model into the 14 candidate models for initial occupancy. At each stage, we identified the best-supported model as the model with the lowest AIC value, excluding models that did not converge, except if there was a simpler nested model among those with $\Delta AIC < 2$. Models include initial occupancy (ψ), colonization (γ), extinction (ϵ), and detection (p) parameters. The notation (.) indicates the parameter was constant. Species include little brown bat (MYOLUC, *Myotis lucifugus*), northern long-eared bat (MYOSEP, *Myotis septentrionalis*), tricolored bat (PERSUB, *Perimyotis subflavus*), and big brown bat (EPTFUS, *Eptesicus fuscus*). Parks include Apostle Islands National Lakeshore (APIS), Grand Portage National Monument (GRPO), Indiana Dunes National Park (INDU), Isle Royale National Park (ISRO), Mississippi National River and Recreation Area (MISS), Pictured Rocks National Lakeshore (PIRO), Saint Croix National Scenic Riverway (SACN), Sleeping Bear Dunes National Lakeshore (SLBE), and Voyageurs National Park (VOYA).

Species	Park	Model structure	nPars	ΔAIC	AIC wt
MYOLUC	APIS	$\psi(.) \gamma(.) \epsilon(.) p(.)$	4	0.00	0.21
	GRPO	$\psi(\text{elevation}) \gamma(.) \epsilon(.) p(\text{days after leaf-out} + \text{year})$	10	0.00	0.42
	INDU	$\psi(\% \text{ open land}) \gamma(.) \epsilon(.) p(\text{temperature} + \text{humidity} + \text{wind} + \text{precipitation} + \text{mic height} + \text{clutter distance} + \text{days after leaf-out} + \text{year})$	16	0.00	0.16
	ISRO	$\psi(\text{elevation}) \gamma(.) \epsilon(.) p(\text{temperature} + \text{humidity} + \text{wind} + \text{precipitation} + \text{mic height} + \text{clutter distance} + \text{days after leaf-out} + \text{year})$	16	0.00	0.95
	MISS	$\psi(\% \text{ open water}) \gamma(.) \epsilon(.) p(.)$	5	0.00	0.33
	PIRO	$\psi(.) \gamma(.) \epsilon(.) p(.)$	4	0.00	0.15
	SACN	$\psi(.) \gamma(.) \epsilon(.) p(\text{temperature} + \text{humidity} + \text{wind} + \text{precipitation} + \text{year})$	11	0.00	0.27
	SLBE	$\psi(\% \text{ open water}) \gamma(.) \epsilon(.) p(\text{mic height})$	6	0.00	0.33
	VOYA	$\psi(.) \gamma(.) \epsilon(.) p(\text{temperature} + \text{humidity} + \text{wind} + \text{precipitation} + \text{mic height} + \text{clutter distance} + \text{days after leaf-out} + \text{year})$	15	0.00	0.23
	APIS	$\psi(\% \text{ open land}) \gamma(.) \epsilon(.) p(\text{clutter distance})$	6	0.00	0.26
MYOSEP	GRPO	$\psi(\% \text{ open water}) \gamma(.) \epsilon(.) p(\text{temperature} + \text{humidity} + \text{wind} + \text{precipitation} + \text{year})$	13	0.06	0.20
	ISRO	$\psi(\% \text{ open water}) \gamma(.) \epsilon(.) p(\text{year})$	9	0.00	0.24
	MISS	$\psi(.) \gamma(.) \epsilon(.) p(.)$	4	0.00	0.20
	VOYA	$\psi(\text{elevation}) \gamma(.) \epsilon(.) p(\text{mic height} + \text{clutter distance} + \text{days after leaf-out})$	8	0.00	0.33
	MISS	$\psi(\% \text{ forest}) \gamma(.) \epsilon(.) p(\text{days after leaf-out} + \text{year})$	9	0.00	0.16
PERSUB	SACN	$\psi(\% \text{ open water}) \gamma(.) \epsilon(.) p(.)$	5	0.37	0.25
	INDU	$\psi(\text{elevation}) \gamma(.) \epsilon(.) p(\text{temperature} + \text{humidity} + \text{wind} + \text{precipitation} + \text{mic height} + \text{clutter distance} + \text{days after leaf-out} + \text{year})$	16	0.00	0.35
	ISRO	$\psi(\% \text{ open land}) \gamma(.) \epsilon(.) p(\text{days after leaf-out})$	6	0.00	0.43
EPTFUS	MISS	$\psi(\% \text{ developed}) \gamma(.) \epsilon(.) p(\text{mic height} + \text{clutter distance})$	7	0.00	0.18
	PIRO	$\psi(\% \text{ open land}) \gamma(.) \epsilon(.) p(.)$	5	1.37	0.15
	SACN	$\psi(\% \text{ developed}) \gamma(.) \epsilon(.) p(\text{temperature} + \text{humidity} + \text{wind} + \text{precipitation} + \text{mic height} + \text{clutter distance})$	11	0.00	0.29
	SLBE	$\psi(\% \text{ open land}) \gamma(.) \epsilon(.) p(\text{temperature} + \text{humidity} + \text{wind} + \text{precipitation} + \text{mic height} + \text{clutter distance} + \text{days after leaf-out} + \text{year})$	15	0.00	0.18

predicted activity estimates for little brown bat ranged from 0.5 to 65.3 calls per detector-night; for northern long-eared bat from 0.1 to 29.7 calls per detector-night; for tricolored bat from 1.1 to 12.1 calls per detector-night; and for big brown bat from 0.6 to 89.1 calls per detector-night. Little brown bat activity declined in all nine parks from the first year of surveys to the last, by 14–91 %. Likewise, northern long-eared bat activity declined by 34–97 % in all five parks where the species was analyzed. For both little brown and northern long-eared bats, the most dramatic declines occurred at GRPO and ISRO. We also observed large declines in tricolored bat activity at both parks that were analyzed, a decrease of 81 % at MISS and 67 % at SACN. Big brown bat was the only species for which we saw an increase in activity, up 16 % on average from the first year to the last year of surveys.

In the best supported activity models, the covariates that were most frequently related to bat activity were survey year, elevation, and percent forest cover (Table 2; Appendix Tables A9, A12). For big brown bat at ISRO, the two models with lowest AIC values did not converge and were excluded from consideration; instead we used the third ranked model which had minimal support based on the AIC weight (Table 2). In models where elevation was significant, it was always inversely related to activity (Appendix Table A9). Activity of little brown bat at APIS and SACN, tricolored bat at SACN, and big brown bat at PIRO were all inversely related to percent forest cover. However, activity of little brown and tricolored bats was positively related to percent forest cover at MISS, the least forested, most urban park.

3.3. Activity-occupancy comparison

Acoustic activity rate and probability of use were positively related; however, it was not a linear relationship (Fig. 3). When relative activity was low (<25 % of maximum activity), probability of use ranged from

Table 2

Best-supported activity model for each park and species. We tested 13 candidate models and identified the best-supported model as the model with the lowest AIC value, excluding models that did not converge, unless there was a simpler nested model among those with $\Delta AIC < 2$. All models included random effects for survey effort and sample site. Species include little brown bat (MYOLUC, *Myotis lucifugus*), northern long-eared bat (MYOSEP, *Myotis septentrionalis*), tricolored bat (PERSUB, *Perimyotis subflavus*), and big brown bat (EPTFUS, *Eptesicus fuscus*). Parks include Apostle Islands National Lakeshore (APIS), Grand Portage National Monument (GRPO), Indiana Dunes National Park (INDU), Isle Royale National Park (ISRO), Mississippi National River and Recreation Area (MISS), Pictured Rocks National Lakeshore (PIRO), Saint Croix National Scenic Riverway (SACN), Sleeping Bear Dunes National Lakeshore (SLBE), and Voyageurs National Park (VOYA).

Species	Park	Model structure	df	$\Delta AICc$	AICw
MYOLUC	APIS	year + % forest	8	0.00	0.24
	GRPO	year + elevation	9	0.97	0.33
	INDU	year	8	0.38	0.16
	ISRO	year + elevation	9	0.00	0.69
	MISS	year + % forest	8	0.00	0.21
	PIRO	year	6	1.53	0.11
MYOSEP	SACN	year + % forest	8	0.00	0.45
	SLBE	year + canopy height	8	0.00	0.21
	VOYA	year + elevation	9	0.00	0.39
	APIS	year	7	1.36	0.13
	GRPO	year + canopy height	9	0.00	0.18
	ISRO	year	8	0.00	0.21
PERSUB	MISS	year + % developed	8	0.00	0.40
	VOYA	year + elevation	9	0.00	0.31
	MISS	year + % forest	8	0.00	0.34
	SACN	year + % forest	8	0.00	0.25
	INDU	year	8	1.60	0.10
	ISRO	year + % forest + canopy height	10	12.16	0.00
EPTFUS	MISS	year	7	0.00	0.24
	PIRO	year + % forest	7	0.00	0.27
	SACN	year + elevation	8	0.00	0.78
	SLBE	year + % open land	8	0.68	0.13

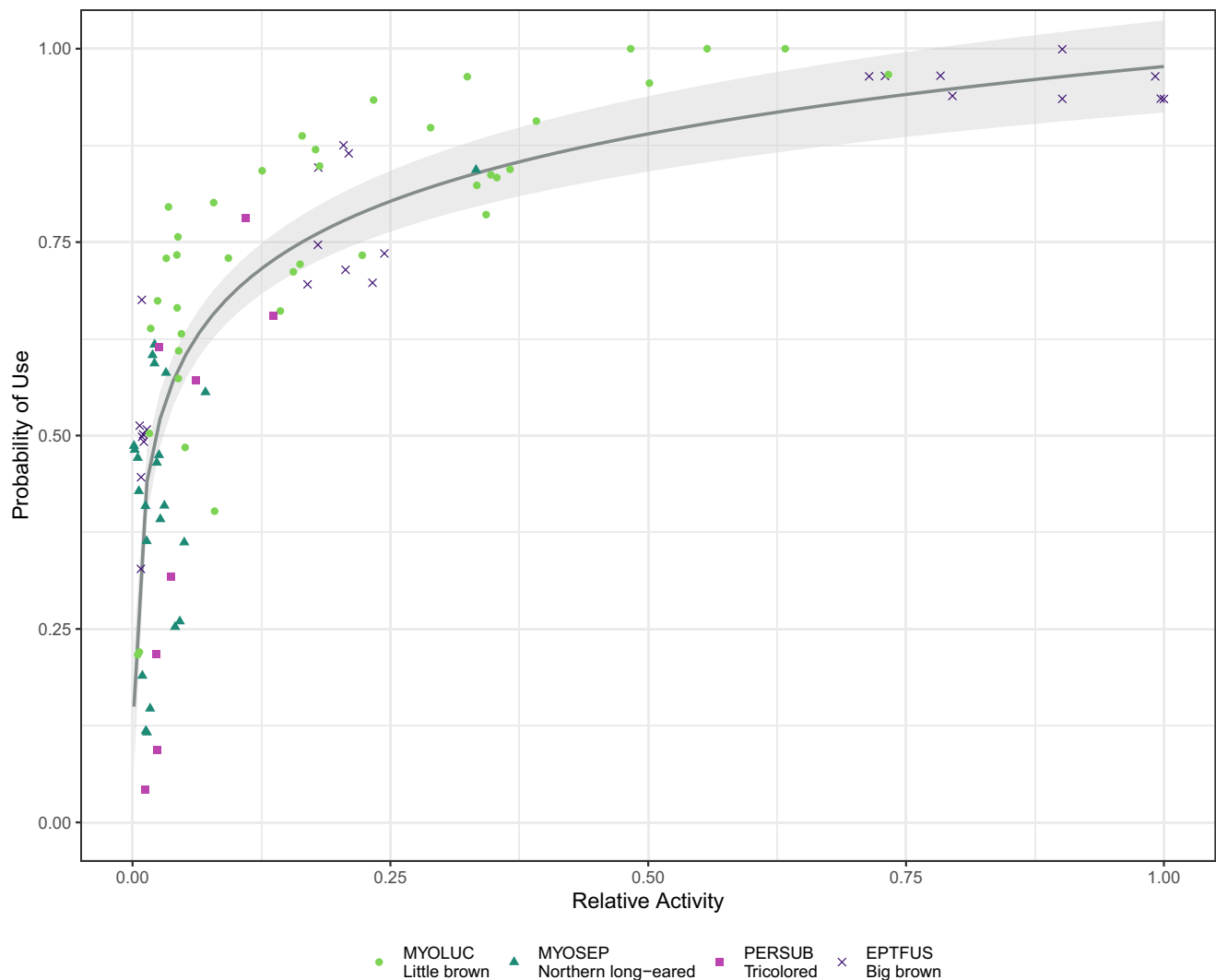


Fig. 3. Relative acoustic activity versus probability of use for each species-park-year combination. Relative activity was calculated as model-predicted activity (mean call files per detector-night) divided by the maximum model-predicted activity of any species-park-year combination. Species include little brown bat (MYOLUC, *Myotis lucifugus*, green circle), northern long-eared bat (MYOSEP, *Myotis septentrionalis*, blue triangle), tricolored bat (PERSUB, *Perimyotis subflavus*, pink square), and big brown bat (EPTFUS, *Eptesicus fuscus*, purple cross). Line represents the smoothed conditional mean from a model with formula $y \sim \log(x)$; gray shading represents standard error around the line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

near zero to 0.75. Thus, low activity did not reliably predict low use. In contrast, when relative activity was high (>75 % of maximum activity), probability of use was also high (0.90 or more). All four species fit this pattern.

4. Discussion

We investigated trends in summer occurrence and activity for four bat species over a broad geographic area, the western Great Lakes region. During a five-year period, we generally observed strongly declining trends in both probability of use and acoustic activity level for little brown, northern long-eared, and tricolored bats. Because our study areas are located in protected national parks, most of which have not experienced major changes to the landscape, and because our focal species are not subject to high fatality rates at wind energy facilities (Choi et al., 2020) the observed declines suggest WNS has negatively impacted these species. Supporting this idea, hibernacula counts in the region also decreased dramatically after the arrival of WNS (Kurta and Smith, 2020). In contrast, we found that big brown bat probability of use and acoustic activity levels generally declined less or increased, which we believe indicates this species has not been as strongly impacted by

WNS.

Little brown bat acoustic activity decreased at all nine parks over the course of our study, while probability of use decreased at eight parks. The declines we observed (14–91 % for activity, 11–56 % for use) were similar to results from other studies (Morningstar et al., 2019; Nocera et al., 2019; Deeley et al., 2021; Udell et al., 2022). For little brown bat, PIRO had the lowest mean probability of use and the lowest mean activity rate out of all parks, however these results may be partially due to the differences in recording of different detector brands (Barr, 2019). Yet, we also observed the largest decline in probability of use at PIRO. We used the same detector brand at PIRO consistently throughout the study, suggesting this within-park trend is valid. Extensive incidence of beech bark disease at PIRO has led to changes in forest structure (Sattler, 2021), which may be negatively affecting availability of little brown bat habitat. INDU, the southernmost park, is the only location where we saw increasing little brown bat use of the area. Based on models predicting WNS spread (Pettit and O'Keefe, 2017; Weins and Thogmartin, 2022), bats at INDU may have been exposed to the disease sooner than at other parks. Following initially severe WNS mortality, there is evidence for increasing survival and stabilization at some little brown bat colonies in the northeastern U.S. (Maslo et al., 2015). Similar processes may explain

increasing use at INDU. We did not see a corresponding increase in activity at INDU, but activity was steady for the last three years of surveys, suggesting the population may be stabilizing and not continuing to decline.

Northern long-eared bat acoustic activity decreased at all parks by 34–97 %, while probability of use decreased at three parks (by 35–78 %) and increased at two (by 6–34 %). The large declines in activity we observed were similar to those in other studies (Deeley et al., 2021; Nocera et al., 2019). Udel et al. (2022) estimated a range-wide 14 % increase in occupancy from 2016 to 2019, midway between the increases we saw at two parks. The mix of positive and negative trends in probability of use that we observed may be related to the use of different hibernacula. Although hibernacula locations are not known for our parks' bat populations, given the northern long-eared bat's maximum dispersal distance of 90 km (Straw et al., 2022), we expect bats from different parks would have little or no overlap in hibernacula sites, and may experience different WNS exposure.

For tricolored bats, there were notable differences between the two parks for which we modeled trends. In 2016, probability of use was more than two times higher, and activity was more than three times higher at MISS than at SACN. Udel et al. (2022) predicted consistently high tricolored bat summer occupancy in southeast Minnesota and southwest Wisconsin, adjacent to MISS. This area contains extensive forest and karst-dominated geology, providing year-round high-quality habitat for tricolored bats (ICF, 2022). We observed a mean 46 % decline in tricolored bat use, compared to 42 % reported by Udel et al. (2022). Likewise, our observed mean decline in activity (74 %) is similar to findings from other regions (Deeley et al., 2021; Nocera et al., 2019).

On average across parks, probability of big brown bat use decreased and activity increased, but the direction of park-specific trends varied. Previous studies comparing pre-WNS to post-WNS activity for big brown bats also found mixed results (Morningstar et al., 2019; Bombaci et al., 2021; Nocera et al., 2019). Our mean yearly probabilities of use for big brown bat (0.71–0.82) were similar to post-WNS probabilities in New York (0.74–0.87; Coleman et al., 2014b). However, probability of use at PIRO declined by >50 % after the first year; no other park's probability for this species changed by >5 %. We hypothesize that PIRO's steep declines in big and little brown bat occurrence could be related to recent changes in forest structure caused by beech bark disease (Sattler, 2021). Low but stable big brown bat use was observed at ISRO, the northernmost and least developed park. This is likely due to limited availability of important habitat features, specifically buildings to roost in (Whitaker and Gummer, 2000) and open land (Ford et al., 2005; Appendix Table A2).

We expected to identify environmental covariates that predicted the probability of a species using an area, given previous work documenting habitat associations (Hein et al., 2009; Blakey et al., 2019). However, we found only one strong relationship (open water predicted probability of tricolored bat use at one park). Analyses by Nocera et al. (2020) and Law et al. (2020) likewise found that environmental variables generally did not influence bat occurrence. Our lack of meaningful covariates predicting probability of bat use can be attributed, in some cases, to very high initial occupancy rates (>0.95). If a species uses all available sites, the sites' environmental characteristics are not informative. Secondly, our models may have captured most of the variation among sites within the detection portion of the model. Survey year (reflecting time since WNS arrival in the region), time of year, proximity to clutter, and microphone height, which varied across sites, were important predictors of detection probability in many of our models.

In contrast to our occupancy models, most activity models included significant environmental covariates (land cover, elevation, or canopy height). Other studies have likewise documented significant relationships between bat activity and land cover (Nocera et al., 2020; Gorman et al., 2022). We found that forest cover predicted activity more frequently than other habitat variables. However, the relationship between forest cover and activity depended on landscape-level context. In

an urban park with minimal forest (MISS), activity was positively related to percent forest cover, but in more forested parks the relationship was negative. We also showed that higher bat activity occurred at lower elevations and taller canopy heights, in accordance with previous findings (Ford et al., 2005; Hein et al., 2009). To summarize, our work corroborates that of Dibner et al. (2017), demonstrating that species occurrence (or use of space) and species abundance have different relationships to environmental covariates.

Our results support the idea that changes in species' use of an area occur on a different temporal scale than changes in activity. As noted by Rodhouse et al. (2015), bat occurrence in an area can change slowly because they are long-lived and have long-term fidelity to roosting and foraging sites. Activity, on the other hand, can change rapidly at the hourly, nightly, or seasonal time scale in relation to weather, prey availability, juvenile recruitment, or migration (Bombaci et al., 2021; Nocera et al., 2019). Secondly, our findings indicate that changes in species' use of an area occur on a different spatial scale than changes in activity. Site-specific landscape and habitat variables significantly influenced the rate of bat activity, but not bat occurrence. We suggest that the occupancy (or use) metric may be better suited for long-term, broader-scale analyses while the activity metric may be better suited for short-term, local-scale analyses.

Previous work linking occurrence and abundance in other species shows these two parameters are often, but not always, positively related (Gaston et al., 2000). Furthermore, the relationship may be either linear (Tempel and Gutierrez, 2013) or nonlinear (Latham et al., 2014). When comparing the outcomes of modeling these two different parameters, we found a positive, nonlinear relationship (Fig. 3) wherein a decline in relative activity did not necessarily signify a corresponding decline in probability of a species using the area. Acoustic activity trends for three bats in our study (little brown, northern long-eared, and tricolored) imply that their populations have experienced precipitous declines. Populations of these three species at hibernacula in the Great Lakes region have also plummeted (Kurta and Smith, 2020). However, our data suggest that despite steep declines, these species maintained high probabilities of summer use across much of the landscape we studied.

Activity and occurrence metrics provide complementary information about bat population status and trends but are not interchangeable and do not reliably predict each other. We showed that acoustic activity is a more sensitive measure of change while species' use of an area is more stable. Tracking bat activity levels could more quickly offer insight into species' changing status, facilitating timely management intervention. However, using an activity metric does not account for, and may be biased by, imperfect detection. While occupancy modeling mitigates for detection bias by explicitly including detectability in the model, it operates on a coarser scale and may not distinguish local-level habitat influences or rapid changes. Understanding these differences provides capacity for land managers and conservation decision-makers to assess their objectives, priorities, and timeline when deciding which analytical method to employ. In light of rapid and widespread global change, it is imperative to collect data on vulnerable wildlife populations in an efficient manner to inform timely and effective conservation solutions.

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CRediT authorship contribution statement

Katy R. Goodwin: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Louis Hunnink:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Conceptualization. **Joy O'Keefe:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Alan Kirschbaum:** Writing – review & editing, Visualization, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **Erin H. Gillam:** Writing –

review & editing, Project administration, Methodology, Funding acquisition. **Cindy Heyd:** Writing – review & editing, Project administration, Methodology, Funding acquisition. **Mark C. Romanski:** Writing – review & editing, Project administration, Methodology, Funding acquisition. **William T. Route:** Writing – review & editing, Project administration, Methodology, Funding acquisition. **Steve K. Windels:** Writing – review & editing, Project administration, Methodology, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data includes sensitive species information. Some data may be made available upon request.

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