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Zackary W. Isenhour^{1,*}, Katherine M. Gorman¹, Megan L. Moran¹,
Hila Taylor¹, and W. Mark Ford²

Abstract – We assessed foraging-habitat associations at the landscape scale for 9 bat species in Maryland and Pennsylvania, U.S.A, from a multi-year perspective. Trends in landscape use included greater acoustic activity of *Eptesicus fuscus* along forest-field edges, rather than within forested habitats, and greater activity of *Lasiurus borealis* in xeric forests, rather than hydric/mesic conditions relative to aspect. Additionally, no species had a meaningful relationship with McNab’s Landform Index. Our results also demonstrated that activity of most species was consistent over the survey period, although some counts were extremely low and attributable, in part, to previous population reductions from white-nose syndrome. Activity levels of *E. fuscus*, *M. lucifugus*, *M. septentrionalis*, *M. sodalis*, and *Perimyotis subflavus* appeared related to the annual reproductive cycle, i.e., pregnancy, lactation, and volancy of pups. Our study indicates that, while activity patterns were generally consistent across years and regions, species-specific responses vary among regions and over time, highlighting the need for multi-year locally focused bat research.

Introduction

Bats in the interior mid-Atlantic region of the United States have become a heightened conservation concern for state and federal biologists tasked with their management. Some cave-hibernating species have experienced population declines of >90% after the advent of white-nose syndrome (WNS) in the United States in winter 2006–2007 (Cheng et al. 2021). Five of the 9 species found in the region have been negatively impacted by WNS: *Eptesicus fuscus* (Palisot de Beauvois) (Big Brown Bat), *Myotis lucifugus* (Le Conte) (Little Brown Bat), *Myotis septentrionalis* (Trouessart) (Northern Long-eared Bat), *Myotis sodalis* Miller and G.M. Allen (Indiana Bat), and *Perimyotis subflavus* (F. Cuvier) (Tricolored Bat). *Eptesicus fuscus* is resistant to infection by *Pseudogymnoascus destructans* (Blehert and Gargas) Minnis and D. L. Lindner, the causative agent of WNS, resulting in less severe declines in populations, relative to other affected species (Moore et al. 2018, Verant et al. 2018). Mortality in WNS-affected populations of myotids, *P. subflavus*, and *E. fuscus* during summer in the Northeast and in the interior mid-Atlantic has resulted in indirect declines in acoustic activity (Deeley et al. 2021, Nocera et al. 2020). Little is known about the only other myotid found in this region, *Myotis leibii* (Audubon and Bachman) (Eastern Small-footed Bat), or its response to WNS (Deeley et al. 2021, Sasse and Perry 2023).

Non-cave-hibernating migratory bats in the interior mid-Atlantic region, including *Lasiurus cinereus* (Palisot de Beauvois) (Hoary Bat), *Lasiurus borealis* (Müller) (Eastern Red Bat), and *Lasionycteris noctivagans* (Le Conte) (Silver-haired Bat), have not been impacted by WNS (Cheng et al. 2021). However, migratory bats are vulnerable to mortality at wind-energy facilities (Weaver et al. 2025), and wind-energy has expanded regionally over the past decade (USDE 2025). Estimates

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based on viability modeling indicate a range-wide population decline of *L. cinereus* by 90% in the next 40 years (Frick et al. 2017a).

Landscape associations are key to understanding bat community compositions, as well as managing for individual species. Some landscape covariates are static, such as topography, whereas others, such as forest structure and composition, can be managed for the benefit of bats. Elevation, for example, has a positive relationship with activity of *M. septentrionalis*, while having a negative relationship with activity of *P. subflavus* (Ford et al. 2005, 2016). Aspect and slope influence temperature and moisture and are significant modifiers of vegetative composition, forest structure, and insect abundance (Ford et al. 2005, True et al. 2023). Types of landform, such as sheltered valleys and coves versus exposed ridges and side slopes, further influence temperature and moisture that, in turn, can affect insect abundance (Ford et al. 2015, McNab 1992). Large-bodied species, such as *E. fuscus*, *L. borealis*, *L. cinereus*, and *L. noctivagans*, are generally associated with open-canopy forests or forest-edge habitats (Fill et al. 2022, Ford et al. 2005), whereas smaller species, such as *M. septentrionalis* and *M. sodalis*, are strongly associated with contiguous forests (Brooks 2009, Ford et al. 2005). Many species have high activity at water features, including *M. lucifugus*, *M. sodalis*, and *P. subflavus*, as these areas typically are associated with insect emergences and serve as a source of drinking water (Cable and Willcox 2024, Coleman et al. 2014, Nocera et al. 2020). Understanding these relationships can inform management efforts and help biologists direct and target monitoring for species of high conservation concern.

Our primary objective was to determine habitat associations of bat species using acoustic activity. Our second objective was to identify trends in activity between years and within season, using our multi-year dataset. This sampling period occurred after most WNS-induced mortality and followed an increase in regional wind-energy development. Consequently, we predicted activity to be lower than pre-WNS values reported by Johnson et al. (2008) for most bats affected by WNS. Additionally, based on previous studies in the region, we predicted activity to continue to decline or, at best, maintain stability relative to pre-WNS values for those same species, excluding *M. lucifugus*. We predicted that acoustic detections of *M. lucifugus* would increase, as others have noted an increase in abundance following initial declines (Cheng et al. 2021, Dobony and Johnson 2018, Frick et al. 2017b). We also anticipated a decline in activity of non-cave-hibernating, migratory species compared to previous regional studies due to increased wind-energy development in the interior mid-Atlantic, particularly in the central Appalachian Mountains to the north and west of our study areas (USDE 2025).

Field-site Description

We conducted our study within 2 sites managed by the National Park Service in the interior mid-Atlantic of the eastern United States: Gettysburg National Military Park and Eisenhower National Historic Site (GETT), in Adams County, Pennsylvania, and Catoctin Mountain Park (CATO), in Fredrick County, Maryland (Fig. 1). The 2 sites are within different physiographic regions; the 2700-ha GETT complex is in the Piedmont Province, and the 2384-ha CATO site is in the Blue Ridge Province (Sevon 2000; Maryland Geological Survey 2008). Dominant forest vegetation at both locations consists of second- or third-growth *Quercus-Carya* (oak-hickory), mesic stands of maple (*Acer*), *Liriodendron tulipifera* L. (Yellow Poplar), *Tsuga canadensis* (L.) Carrière (Eastern Hemlock), and *Pinus strobus* Linnaeus (Eastern White Pine) (Braun 1950, Dyer 2006). Forested habitat at CATO is continuous and constitutes ~98 percent of the park's land cover (USGS 2024). As a historic battlefield, maintained open areas (i.e., fields and croplands) are a significant habitat component at GETT (~46 percent, USGS 2024). Moreover, in contrast to CATO, much of the area surrounding GETT is developed, consisting of suburban and urban land use. Elevation ranges

from 128 m to 238 m at GETT and from 194 m to 574 m at CATO (USGS 2023). The topography at CATO is mountainous and rugged, whereas GETT generally has a rolling landscape, although some localized areas of steep relief occur (USGS 2023). Due to small size of the northwestern parcel and forest fragmentation in both the far eastern and northwestern parcels of GETT (<10% forest cover each), these parcels were not surveyed (Fig. 1).

The bat community in Pennsylvania and Maryland is composed of 9 regularly occurring species, including *M. lucifugus*, *M. septentrionalis*, *M. sodalis*, *M. leibii*, *E. fuscus*, *P. subflavus*, *L. noctivagans*, *L. borealis*, and *L. cinereus* (Deeley et al. 2022). Several species, including *M. sodalis* and *M. septentrionalis*, are listed as endangered or otherwise imperiled at the federal or state level, and regional populations have experienced substantial declines in recent decades (USFWS 2024a).

Methods

Field data collection

To account for potential bias that may result from single-year sampling (Russo-Petrick and Root 2025), we monitored acoustic activity from 15 May to 15 August 2022–2024 (USFWS 2024a), using bat detectors (SM4-ZCs paired with SMM-U1 external microphones; Wildlife Acoustics, Maynard, MA). We deployed detectors simultaneously at CATO ($n = 18$) and GETT ($n = 22$). We distributed detectors among land-cover types in proportion to their availability within each park, to ensure adequate representation of all habitats. At GETT, 9 detectors were deployed along forest-field edges, and 13 were placed within forests. In contrast, CATO is predominantly forested; therefore, 15 detectors were placed within forests, and only 3 were deployed along forest-field edges. We deployed bat detectors at sites along road corridors, field edges, and over streams to ensure re-

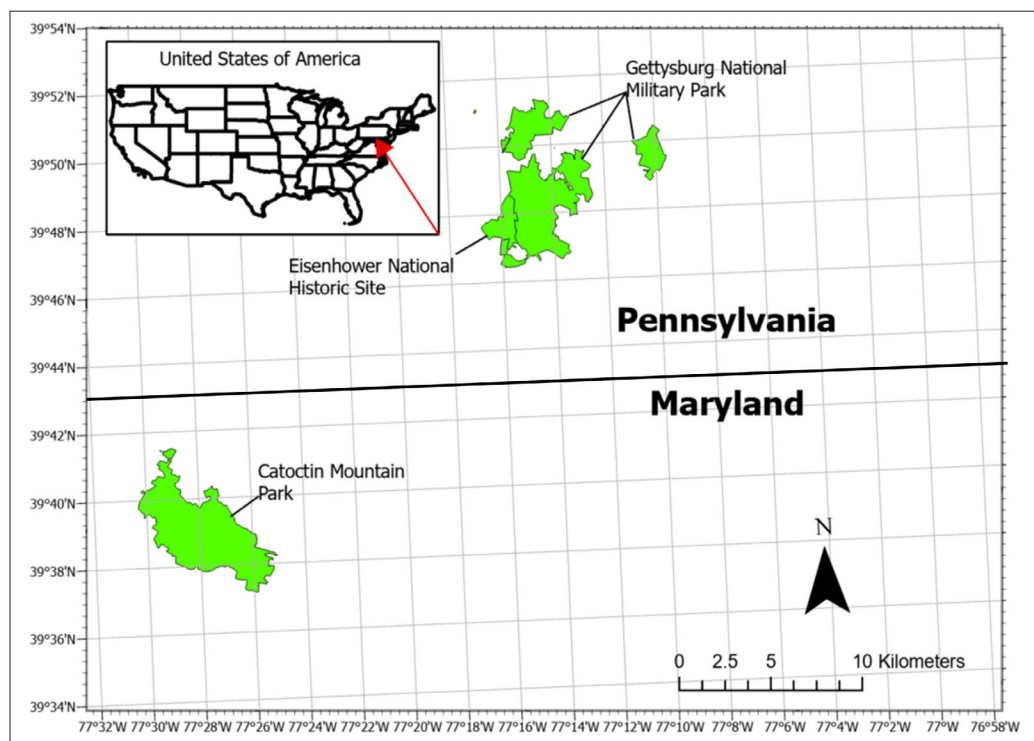


Figure 1. National Park Service study area locations: Catoclin Mountain Park, Maryland, Eisenhower National Historic Site and Gettysburg National Military Park, Pennsylvania.

cording of high-quality echolocation passes and maximize detection capability (Loeb et al. 2015). Microphones were mounted on 3.3-m extendable poles and directed into the flyway (Loeb et al. 2015). We minimized detection error by sampling the same location each year for the duration of the study. We programmed detectors to record from 60 min before sunset until 60 min after sunrise. Sampling occurred on a minimum of 60 nights at each detector location for each sampling year.

We identified recorded calls to species using Kaleidoscope Pro v5.6.8 and classifier v5.4.0 (Wildlife Acoustics), with sensitivity set to 0. To account for potential misidentifications and increase accuracy, we set a minimum threshold of 3 pulses per call file for inclusion in species identification (Mutthersbaugh et al. 2019) and only retained the nightly species counts produced by Kaleidoscope Pro when the maximum likelihood estimates (MLE) calculated by the software had P -values < 0.05 (Ford et al. 2023, Isenhour et al. 2026). We visually vetted calls identified as *M. sodalis*, as well as all other myotids and *P. subflavus*, using quantitative metrics (e.g., minimum and mean call note frequency, and call note curvature and slope) in a dichotomous key for bats in the eastern United States (Johnson et al. 2013). Although the calls of *M. sodalis* and *M. lucifugus* are very similar, we chose not to lump them into a single category, in order to assess more clearly variation in habitat use between the 2 species.

Statistical analysis

We assembled a suite of landscape covariates for each site prior to analysis. We extracted elevation for each detector location from digital elevation models (DEM), with 1-m resolution (USGS 2023). For each location, we calculated aspect and slope in degrees from these DEMs in R package *terra* (Hijmans 2025, R Core Team 2023). As aspect is a circular variable, we conducted a sine and cosine transformation to ensure values were cyclic, with the sine-transformed data representing easting and cosine-transformed data representing northing (True et al. 2023). We calculated landform index (LFI), which is a measure of landform shape (i.e., flat, concave, convex), in ArcGIS Pro (Version 3.2.2; ESRI, Redlands, CA), following the methods of McNab (1992), as modified for geographic information systems by Odom et al. (2001). We calculated the Euclidean distance to water from each detector location using the *terra* package (Hijmans 2025) and the National Wetland Inventory (NWI) program (USFWS 2024b). Areas of forest and edge were determined with data from the 30-m resolution Multi-Resolution Land Characteristics National Land Cover Database (USGS 2024). Anthropogenic land cover was excluded as it consisted of only small portions of both parks (e.g., GETT ~5% non-vegetated area, including water; CATO ~2% non-vegetated area, including water).

All statistical analyses were performed in R (R Core Team 2023). We used generalized linear mixed models to analyze activity at the species level, using the package *glmmTMB* (Brooks et al. 2017). We assessed correlations between predictor variables prior to model development with standard correlation tests. Elevation was correlated with project area ($P \geq 0.6$), so we removed elevation to reduce multicollinearity in our models (Saccetti et al. 2020). For all models, we used a negative binomial distribution as the best fit, and we included detector location as a random effect to correct for pseudoreplication.

For model development, we established a common baseline model and a null model for each species. Our baseline model included numerical day of year, quadratic day, year, and park. We then developed *a priori* a series of generalized linear mixed models that contained various environmental covariates added to the baseline model covariates for each species. *A priori* models were derived by grouping similar covariates (e.g., topographic covariates, landscape covariates) and evaluating the models to identify best-fit models (Table 1). Lastly, we constructed a global model for each species containing the baseline model covariates and all environmental covariates. We assessed model fit in packages *DHARMA* and *MuMIn* (Barton 2025, Hartig 2024). We selected top-competing mod-

els for each species using Akaike’s information criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). We considered a candidate model within 2 AICc units of the top model to be competing and potentially informative. If a model was found to be a competing top model, we performed weighted model prediction averaging for final predictions (Cade 2015). We then analyzed each model for spatial autocorrelation using Moran’s I and assessed its significance using a Monte Carlo simulation with 999 iterations and a 5-km spatial weight matrix in R package *spdep* (Bivand and Wong 2018).

We plotted activity against all covariates, with 95% confidence intervals, for visual interpretation of the relationships and identification of trends related to objectives 1 (habitat associations) and 2 (temporal patterns). We then used model predictions to create maps for all myotids and *P. subflavus*, illustrating varying levels of predicted activity across the landscape, supplementing our first objective. Lastly, we developed a Pearson’s correlation matrix to measure pattern similarities of relative abundance between model predictions of each myotid species and *P. subflavus*.

Results

We retained 170,373 acoustic files from CATO and 135,572 from GETT that were obtained during 6869 detector nights (Table 1). Of these, *E. fuscus*, *L. borealis*, *L. cinereus*, *L. noctivagans*, *M. leibii*, *M. lucifugus*, *M. septentrionalis*, *M. sodalis*, and *P. subflavus* had a suitable number of detections for modeling of landscape association. The number of detections for *M. sodalis* at GETT was too low for modeling, nor could the *M. sodalis* files from GETT be confidently verified to species. Only 110 *M. leibii* calls were recorded, which was insufficient for modeling. No models for any species were spatially autocorrelated.

For all species, there was a series of top competing models (Table 2). At CATO and GETT, topographic covariates were highly associated with activity levels for some species. Activity of *M. lucifugus* was negatively associated with slope (see Table S1 in Supplemental File 1, available online at <http://www.eaglehill.us/NABRonline/suppl-files/nabr-037-isenhour-s1.pdf>), and this was the only species for which proximity to water was informative; surprisingly, *M. lucifugus* was recorded more frequently in areas away from water (Table S1). General habitat associations from our models suggested that greater *M. lucifugus* activity was associated with less topographically complex areas and locations away from water. Predicted activity of *M. septentrionalis* was similar to that of *M. lucifugus* (Fig. 2), and visually, all *Myotis* species appeared to use similar areas of GETT (Fig. 2). In addition, *M. septentrionalis* and *M. sodalis* were using similar areas of CATO (Fig. 3).

Table 1. Number and percent of call files identified by for each bat species by project area, in Maryland and Pennsylvania, 15 May–15 August 2022–2024. CATO = Catoctin Mountain Park. GETT = Gettysburg National Military Park and Eisenhower National Historic Site.

Species	CATO (count/percent)	GETT (count/percent)
<i>Eptesicus fuscus</i>	102,610/60.23	103,809/76.57
<i>Lasiurus borealis</i>	7589/4.45	3721/2.74
<i>Lasiurus cinereus</i>	21,627/12.69	10,924/8.06
<i>Lasionycteris noctivagans</i>	19,280/11.32	7774/5.73
<i>Myotis leibii</i>	96/0.06	14/0.01
<i>Myotis lucifugus</i>	16,016/9.40	5735/4.23
<i>Myotis septentrionalis</i>	1398/0.82	214/0.16
<i>Myotis sodalis</i>	1108/0.65	12/0.01
<i>Perimyotis subflavus</i>	649/0.38	3369/2.49
Total	170,373/100	135,572/100

Activity of *E. fuscus* and *P. subflavus* was positively associated with west-facing slopes (Table S1). At GETT, activity of *P. subflavus* was greater near freshwater streams, and at CATO, *P. sub-*

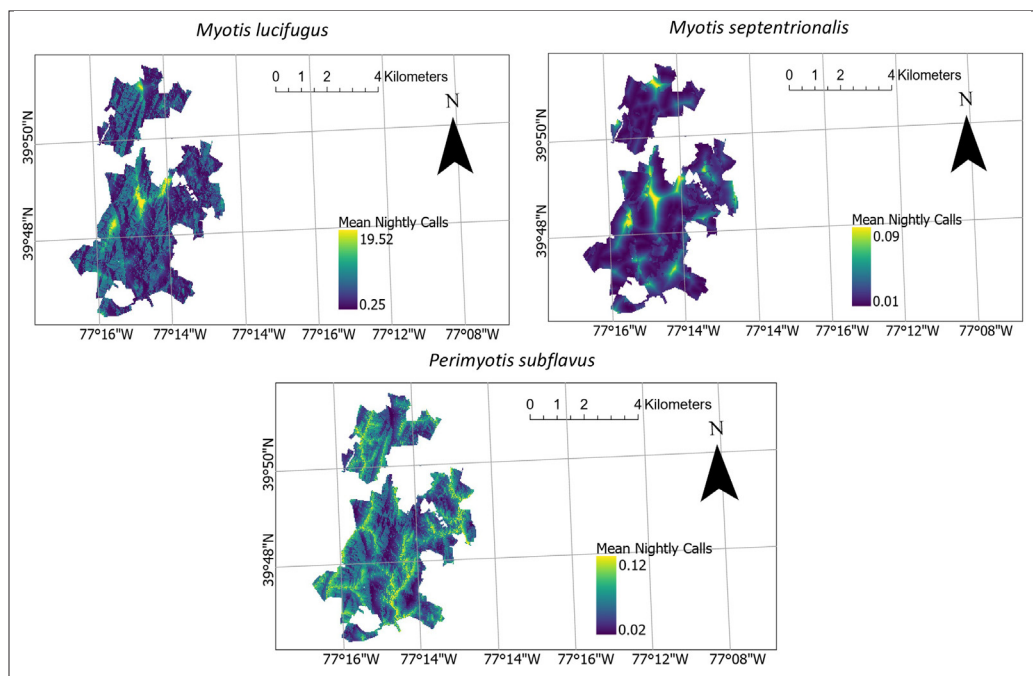


Figure 2. Predicted mean nightly acoustic activity from generalized linear mixed models for *Myotis lucifugus*, *M. septentrionalis*, and *Perimyotis subflavus*, across the landscape at Gettysburg National Military Park and Eisenhower National Historic Site, Pennsylvania.

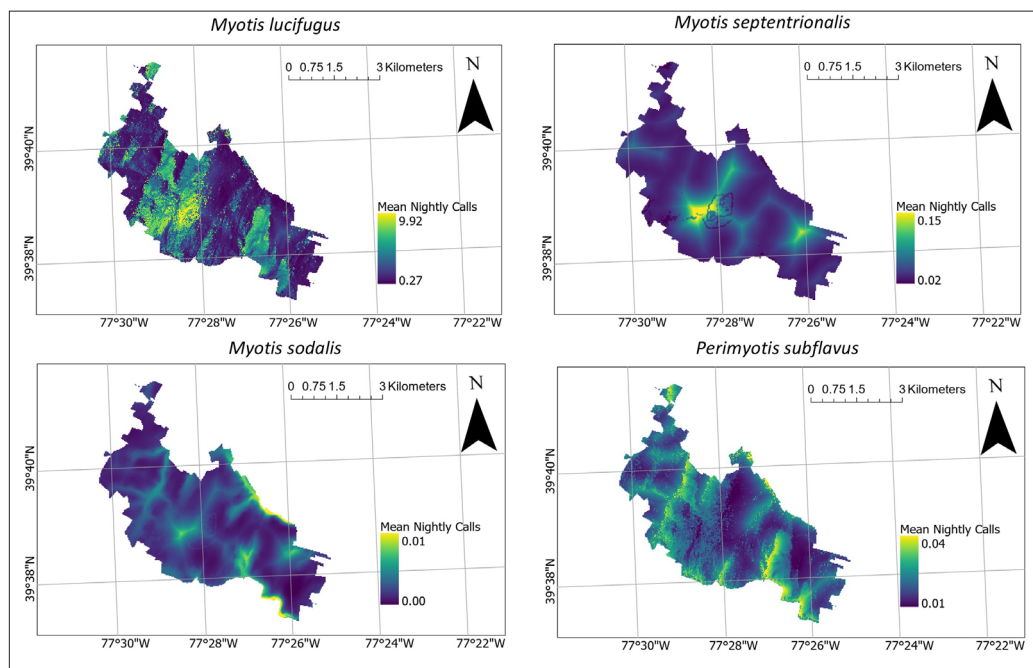


Figure 3. Predicted mean nightly acoustic activity from generalized linear mixed models for *Myotis lucifugus*, *M. septentrionalis*, *M. sodalis*, and *Perimyotis subflavus*, across the landscape at Catocin Mountain Park, Maryland.

Table 2. A priori model selection results of environmental variables predicting acoustic activity for bat species in the interior mid-Atlantic, Maryland and Pennsylvania, 15 May–15 August 2022–2024. Associated number of parameters (K), change in Akaike's information criterion corrected for small sample sizes values (ΔAIC_c), and model weights are also included. Landform index is abbreviated as LFI. Model weights are calculated for the top competing model(s) for each species.

Species	Model	K	ΔAIC_c	Model weight
<i>Eptesicus fuscus</i>				
	Year + Day + Day ² + Project area	4	0.00	0.32
	Year + Day + Day ² + Project area + Distance to water	5	0.81	0.21
	Year + Day + Day ² + Project area + Land cover	5	1.25	0.17
	Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine)	7	1.37	0.16
	Year + Day + Day ² + Project area + LFI	5	1.54	0.15
	Year + Day + Day ² + Project area + Land cover + Distance to water	6	2.13	
	Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine) + LFI	8	2.51	
	Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine) + LFI + Distance to water + Land cover	10	3.58	
	Null	0	1706.64	
<i>Lasius borealis</i>				
	Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine)	7	0.00	0.42
	Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine) + LFI + Distance to water + Land cover	10	0.22	0.37
	Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine) + LFI	8	1.41	0.21
	Year + Day + Day ² + Project area + Distance to water	5	4.81	
	Year + Day + Day ² + Project area	4	5.02	
	Year + Day + Day ² + Project area + Land cover	5	5.58	
	Year + Day + Day ² + Project area + Land cover + Distance to water	6	5.58	
	Year + Day + Day ² + Project area + LFI	5	6.77	
	Null	0	771.66	
<i>Lasius cinereus</i>				
	Year + Day + Day ² + Project area + Land cover	5	0.00	0.61
	Year + Day + Day ² + Project area + Land cover + Distance to water	6	0.88	0.39
	Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine) + LFI + Distance to water + Land cover	10	2.13	
	Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine) + LFI	8	6.36	
	Year + Day + Day ² + Project area	4	7.28	
	Year + Day + Day ² + Project area + LFI	5	7.72	
	Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine)	7	7.74	
	Year + Day + Day ² + Project area + Distance to water	5	7.95	
	Null	0	482.22	
<i>Lastonycteris noctivagans</i>				
	Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine) + LFI + Distance to water + Land cover	10	0.00	0.59
	Year + Day + Day ² + Project area + Land cover	5	0.80	0.41
	Year + Day + Day ² + Project area + Land cover + Distance to water	6	2.80	
	Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine)	7	2.02	
	Year + Day + Day ² + Project area	4	12.81	
	Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine) + LFI	8	13.95	
	Year + Day + Day ² + Project area + Distance to water	5	14.73	
	Year + Day + Day ² + Project area + LFI	5	14.81	
	Null	0	340.92	

Table 2, continued

Species Model	K	ΔAICc	Model weight
<i>Myotis lucifugus</i>			
Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine)	7	0.00	0.49
Year + Day + Day ² + Project area + Distance to water	5	0.87	0.32
Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine) + LFI	8	1.98	0.18
Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine) + LFI + Distance to water + Land cover	10	2.80	
Year + Day + Day ² + Project area + Land cover + Distance to water	6	2.87	
Year + Day + Day ² + Project area	4	2.89	
Year + Day + Day ² + Project area + Land cover	5	4.85	
Year + Day + Day ² + Project area + LFI	5	4.87	
Null	0	1027.05	
<i>Myotis septentrionalis</i>			
Year + Day + Day ² + Project area	4	0.00	0.29
Year + Day + Day ² + Project area + Distance to water	5	0.28	0.25
Year + Day + Day ² + Project area + Land cover + Distance to water	6	0.89	0.18
Year + Day + Day ² + Project area + Land cover	5	1.07	0.17
Year + Day + Day ² + Project area + LFI	5	1.79	0.12
Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine)	7	3.29	
Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine) + LFI + Distance to water + Land cover	10	3.81	
Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine) + LFI	8	4.77	
Null	0	333.37	
<i>Myotis sodalis</i>			
Year + Day + Day ² + Project area	4	0.00	0.44
Year + Day + Day ² + Project area + LFI	5	1.36	0.22
Year + Day + Day ² + Project area + Distance to water	5	1.72	0.18
Year + Day + Day ² + Project area + Land cover	5	1.96	0.16
Year + Day + Day ² + Project area + Land cover + Distance to water	6	3.69	
Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine)	7	4.70	
Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine) + LFI	8	5.61	
Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine) + LFI + Distance to water + Land cover	10	8.76	
Null	0	296.88	
<i>Perimyotis subflavus</i>			
Year + Day + Day ² + Project area + Distance to water	5	0.00	0.26
Year + Day + Day ² + Project area	4	0.29	0.23
Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine)	7	0.62	0.19
Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine) + LFI	8	1.53	0.12
Year + Day + Day ² + Project area + LFI	5	1.66	0.11
Year + Day + Day ² + Project area + Land cover + Distance to water	6	1.93	0.10
Year + Day + Day ² + Project area + Land cover	5	2.23	
Year + Day + Day ² + Project area + Slope + Aspect (sine) + Aspect (cosine) + LFI + Distance to water + Land cover	10	4.66	
Null	0	305.27	

flavus activity was dispersed across the western and eastern regions, similar to freshwater stream locations. Both *L. cinereus* and *L. noctivagans* were detected more frequently in edge habitat than in forested habitat (Table S1). Activity of *L. borealis* was positively associated with south- and east-facing slopes (Table S1). No other species showed a relationship with slope, and no species had significant relationships with aspect or LFI (Table S1).

For GETT, Pearson's correlation matrix showed the most similar model predictions between *M. sodalis* and *M. septentrionalis* (41%; $P < 0.001$), followed by *P. subflavus* and *M. septentrionalis* (39%; $P < 0.001$), and finally between *P. subflavus* and *M. lucifugus* (32%; $P < 0.001$). The correlation matrix at CATO showed the highest similarity between *P. subflavus* and *M. lucifugus* and between *P. subflavus* and *M. septentrionalis* (both 51%; $P < 0.001$), followed by *M. lucifugus* and *M. septentrionalis* (18%; $P < 0.001$). *Myotis sodalis* was least similar to other species, with only 5% similarity between *M. lucifugus* and *M. septentrionalis* ($P < 0.001$).

Activity of *E. fuscus* was statistically higher at GETT than CATO in all top competing models, whereas *L. borealis* and *P. subflavus* showed statistically higher activity at GETT than CATO in 1 of 3 and 1 of 6 top competing models, respectively. Activity of all other species did not vary between GETT and CATO (Fig. 4, Table S1).

Across the study area, we detected overall increased activity for *E. fuscus*, *L. cinereus*, *M. septentrionalis*, and *M. sodalis* from 2022 to 2024 (Fig. 4, Table S1). There was a decline in activity from 2022 to 2023, followed by an increase in 2024 for *L. borealis*, *L. cinereus*, *L. noctivagans*, *M. lucifugus*, and *P. subflavus*. However, activity of both *L. borealis* and *P. subflavus* was still lower in 2024 than 2022 (Fig. 4, Table S1).

Activity of *E. fuscus*, *M. lucifugus*, *M. septentrionalis*, *M. sodalis*, and *P. subflavus* generally increased across the survey season within years, whereas it decreased across season for *L. cinereus*

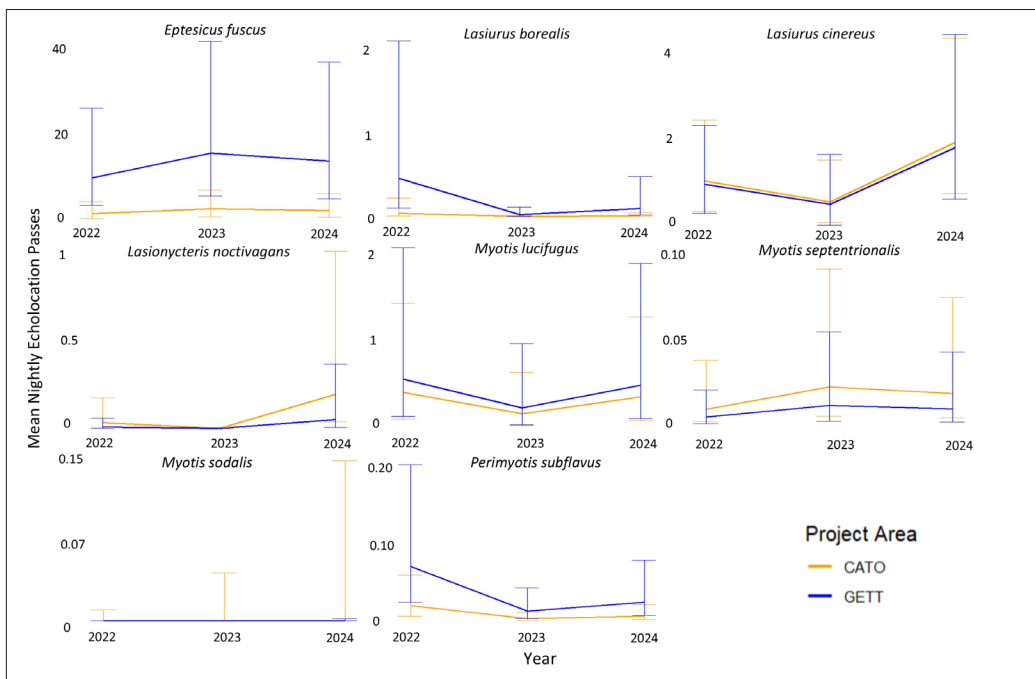


Figure 4. Predicted mean nightly acoustic activity in relation to year, with 95% confidence intervals, from generalized linear mixed models, for all surveyed bat species, excluding *Myotis sodalis*. Data represent 6869 survey nights, from 15 May to 15 August 2022–2024, at Catocin Mountain Park, Maryland (CATO), and Eisenhower National Historic Site and Gettysburg National Military Park, Pennsylvania (GETT).

and *L. noctivagans* (Fig. 5, Table S1). Activity of *E. fuscus*, *L. cinereus*, *M. lucifugus*, and *M. septentrionalis* peaked in the mid-survey season, whereas that of *M. sodalis* and *P. subflavus* peaked near the beginning and end of the season, with lower detection rates in the middle of the survey season (Fig. 5, Table S1). The large error margin of our model predictions for activity of *M. sodalis* relative to numerical day of year made definitive interpretation unreliable (Fig. 5).

Discussion

This multi-year acoustic-monitoring study revealed species-specific habitat associations and temporal activity patterns among bats at CATO and GETT, highlighting the importance of maintaining heterogeneous landscapes to support regional bat diversity. Additionally, this study reflected the utility of multi-season surveys.

Habitat associations varied among species, with differences in activity related to habitat type, landscape position, and survey site. *E. fuscus* had no significant interaction with habitat type, but activity was greater at the less forested GETT than CATO, consistent with the species' demonstrated preference for edge habitat (Fill et al. 2022, Ford et al. 2005). Neither *L. cinereus* nor *L. noctivagans* had a significant difference in activity between CATO and GETT, although activity of both species was more strongly associated with forest-field edges than forested landcover (Fill et al. 2022, Ford et al. 2005). Our use of a survey-site random factor possibly encompassed most of the project area variance, thereby making it difficult to tease out weaker covariate relationships with bat activity (Oberpriller et al. 2022). Although *M. lucifugus* is known to forage over open water (Nelson and Gillam 2017), we observed greater activity in areas distant from water. This may be indicative of day-roost locations, flight corridors leading to foraging areas, or preferred foraging habitat. *L. borealis* and *P. subflavus* exhibited greater activity on xeric slopes, contrary to

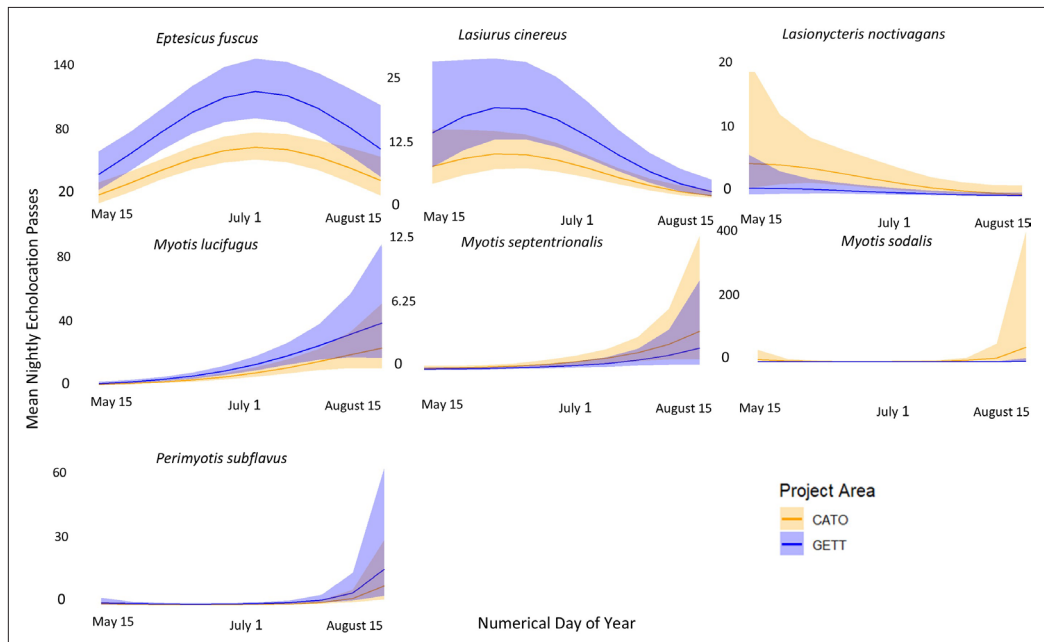


Figure 5. Predicted mean nightly bat acoustic activity in relation to numerical day of year with 95% confidence intervals from generalized linear mixed models for all surveyed bat species, excluding *Lasiurus borealis* and *Myotis sodalis*. Data represent 6869 survey nights, from 15 May to 15 August 2022–2024, at Catoctin Mountain Park, Maryland, and Eisenhower National Historic Site and Gettysburg National

some findings (Ford et al. 2005, 2016), though consistent with others (Austin et al. 2018). These environments might have facilitated insect production and activity, making them attractive to foraging bats (Austin et al. 2018).

We found that year-to-year trends in acoustic activity were variable among species in our study areas. Activity of cave-hibernating species, including *E. fuscus*, *M. lucifugus*, *M. septentrionalis*, and *M. sodalis*, showed a slight increase on the landscape since 2022. At CATO and GETT, *M. lucifugus* activity increased, though levels were still low relative to pre-WNS data from both the Northeast and interior mid-Atlantic (Deeley et al. 2021, Nocera et al. 2019). Decreased acoustic detections of *L. borealis* and *P. subflavus* could be indicative of continued population declines related to wind energy. Acoustic activity of most species, including *L. borealis*, *L. cinereus*, *L. noctivagans*, *M. lucifugus*, *M. septentrionalis*, *M. sodalis*, and *P. subflavus* fluctuated less than a single call per night per bat detector over the 3 years. Activity levels of *M. lucifugus*, *M. septentrionalis*, *M. sodalis*, and *P. subflavus* remained drastically below pre-WNS acoustic levels, as noted by previous workers in the region (Deeley et al. 2021, Nocera et al. 2019).

Equivocal relationships between the numerical day of year and the quadratic day in activity models of *L. borealis* suggested that this species was present on the landscape throughout the duration of our study each year. This was likely because these bats had already migrated to the project area before recording started or they maintained a year-round presence (Johnson et al. 2011). Intra-seasonal trends of *M. septentrionalis* activity in our study were much different than in nearby West Virginia, where Francl et al. (2012) observed a peak in activity during late spring and early summer. This difference could be due to methodological approaches, as Francl et al. (2012) sampled activity via mist netting rather than bat detectors. Positive relationships between the activity of *E. fuscus*, *M. lucifugus*, *M. septentrionalis*, *M. sodalis*, and *P. subflavus* and the numerical day of year could indicate late-season activity of volant pups or species dispersal (Agosta et al. 2005, Cope and Humphrey 2003, Deeley et al. 2022). The negative relationship between *E. fuscus* activity and quadratic day might have been due to earlier successful volancy of pups, followed by the dispersion of maternity colonies across the landscape before surveying concluded, whereas the peak in *L. cinereus* activity relative to quadratic day was possibly due to later migration trends (Cryan et al. 2014, Deeley et al. 2022). Similarly, the steady decline of activity by *L. noctivagans* across the active season was likely due to late spring and early summer northward migration trends, with a slow taper in activity levels as the bats spread across the landscape (Agosta et al. 2005, Cope and Humphrey 2003). The positive relationship between *P. subflavus* activity and quadratic day was probably due to new bats appearing on the landscape, after dispersal from maternity colonies and as bats began moving toward hibernacula for fall swarm (Agosta et al. 2005).

We positively identified *M. sodalis* acoustic files within the CATO project area after manually vetting acoustic calls. While call misidentification can occur—particularly in cluttered habitats where calls may be distorted (Broders et al. 2004, Patriquin et al. 2003)—CATO had an open under- and mid-story, reducing the effects of clutter on call morphology. Areas of high activity of this bat would also be difficult to sample via mist netting due to the open under- and mid-story. Thus, it was possible that limitations of mist netting resulted in an assumption of false absence and underdetection of *M. sodalis* in the local area in earlier studies (Hohoff and Deppe 2024). Lastly, most areas of high activity by *M. sodalis* were along the edge of CATO, suggesting these bats were not using the park extensively; rather, they possibly were more active towards the base of a mountain beyond National Park Service land. Taken together, these lines of evidence indicated that detections of *M. sodalis* were likely correct, but the bats could represent transient, non-reproducing individuals, rather than summer residents.

As nearly 20 years have passed since the introduction of WNS in the region, it is important to reassess our knowledge of habitat use following population declines of several previously

abundant species (Deeley et al. 2021, Johnson et al. 2008). Our multi-year study provides a representative analysis of bat-habitat associations that account for annual variation and single-season bias (Russo-Petrick and Root 2025). Cave-hibernating species, such as *E. fuscus* and *M. lucifugus*, show modest increases in activity consistent with gradual regional recovery, whereas migratory and foliage-roosting species display greater interannual variability, likely driven by weather and movement patterns rather than population shifts (Kurta et al. 2018). To obtain accurate estimates for migratory bats using acoustics, we suggest that monitoring precede and extend beyond the U.S. Fish and Wildlife Service survey window of 15 May–15 August (USFWS 2024a).

Our findings further illustrate that habitat associations differ markedly among species and between project areas, emphasizing that management actions beneficial to 1 species or site may not translate broadly across the landscape. The contrasting landscape structures of CATO and GETT appear to function complementarily, providing nearby habitats that support regional bat diversity. Our results underscore the value of maintaining heterogeneous habitat conditions across nearby landscapes to accommodate differing ecological requirements among species.

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