Relative Activity of Three Bat Species Impacted by White-nose Syndrome on the Chesapeake and Ohio Canal National Historical Park

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Abstract - White-nose syndrome, a disease caused by the fungal-pathogen *Pseudogymnoascus destructans*, has caused drastic reductions in populations of several North American hibernating species of bats including *Myotis lucifugus* (Little Brown Bat), *Myotis septentrionalis* (Northern Long-eared Bat), and *Perimyotis subflavus* (Tricolored Bat). Recent data indicate that populations of Little Brown Bats may be stabilizing and/or increasing in the northeastern region of the US, while others, such as Northern Long-eared Bats, continue to decline. Whether these trends extend to the mid-Atlantic region is currently unknown. To better understand population changes over time, habitat associations, and species dynamics, we developed models of relative activity from bat acoustic data collected on the National Park Service's Chesapeake and Ohio Canal National Historical Park along the Potomac River Corridor in western Maryland between 2016 and 2022. Consistent with pre-disease habitat associations, Little Brown Bats and Tricolored Bats exhibited a positive correlation with proximity to water bodies. Notably, we found Little Brown Bat and Tricolored Bat populations potentially were increasing, whereas Northern Long-eared Bats showed no correlation with examined habitat covariates and had low detection levels, trends consistent with broader declines throughout their range.

Introduction

Bat species in North America have suffered dramatic population declines due to hibernacula disturbance, white-nose syndrome (WNS), wind energy development, and habitat loss/fragmentation and urbanization (Cheng et al. 2021, Deeley et al. 2021, Frick et al. 2010, Langwig et al. 2012, Loeb et al. 2009, True et al. 2021). Hibernating bat species have been severely impacted by the emergence of a fungal pathogen, *Pseudogymnoascus destructans* (Blehert & Gargas) Minnis & D.L. Lindner (*Pd*), the causative agent of WNS (Cheng et al. 2021, Lorch et al. 2011, Warnecke et al. 2012). The fungus produces lesions on the wing, face, and ear membrane, causing infected bats to awaken more frequently from hibernation, which results in loss of critical fat stores, dehydration, and ultimately elevated overwintering morbidity and mortality. Infected bats that survive infection during hibernation may experience reduced reproductive fitness due to their weakened

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Manuscript Editor: Teague O'Mara

condition following hibernation (Blehert et al. 2009, Francl et al. 2012, Gargas et al. 2009, Lorch et al. 2011, Warnecke et al. 2012). Since its discovery in upstate New York in 2006, WNS has caused an estimated 90% decline in the total number of *Myotis lucifugus* (Le Conte) (Little Brown Bat) and *Perimyotis subflavus* (Cuvier) (Tricolored Bat) in eastern North America, triggering a Species Status Assessment review by the US Fish and Wildlife Service (Cheng et al. 2021, Straw et al. 2022). *Myotis septentrionalis* (Trouessart) (Northern Long-eared Bat) are estimated to have declined by 97–100% across 79% of the species' range, resulting in its listing as endangered in the US in 2022 (Cheng et al. 2021, USFWS 2022). WNS-caused mortality has resulted in changes in activity patterns, abundance, local and regional distribution, and inter-specific relationships, including changes in habitat selection, and altered spatial and temporal niche partitioning among both affected and unaffected bat species (Blehert et al. 2009, Brooks 2011, De La Cruz 2024, Ford et al. 2011, Frick et al. 2010, Jachowski et al. 2014).

In addition to WNS, habitat change and forest fragmentation have further affected bat abundance and local to regional bat assemblage and community structure (Coleman and Barclay 2011, Deeley et al. 2021, Johnson et al. 2008, Loeb and O'Keefe 2006, Loeb et al. 2009). Particularly acute in the mid-Atlantic region of the US, expanding urbanization can dramatically impact the quality and availability of foraging habitat, flight corridors, and roosts, translating to changes in patterns of activity and foraging ecology of bats in these areas (Bradley and Altizer 2007, Schimpp et al. 2018). Bat species vary widely in their ability to use landscapes that vary from relatively intact to highly modified. While some bat species, such as *Eptesicus fuscus* (Palisot de Beauvois) (Big Brown Bat), are well adapted to urban environments for both day roosting and foraging (Duchamp and Swihart 2008, Gaisler et al. 1998, Jung and Threlfall 2016, Kurta and Teramino 1992), this pattern is not representative of many North American bat species, particularly those most impacted by WNS. In contrast, species such as the Little Brown Bat, Tricolored Bat, and Northern Long-eared Bat exhibit more complex and often constrained responses to urbanization. For example, Little Brown Bats frequently roost in anthropogenic structures, including barns, houses, and transportation infrastructure (Coleman and Barclay 2011, Fenton and Barclay 1980). However, they typically forage within forests, riparian corridors, and wetlands (Coleman et al. 2014, Ford et al. 2005, Litterer 2024, Menzel et al. 2005, Nocera et al. 2020, Zimmerman and Glanz 2000), habitats that may be limited or fragmented in densely developed urban landscapes. Tricolored Bats are associated with forests and riparian zones, though studies from the mid-Atlantic region found that nightly activity was not significantly influenced by fragmentation or urbanization alone and was higher in fragmented urban parks than in fragmented rural parks (Ford et al. 2005, Johnson et al. 2008). This pattern suggests greater tolerance of altered landscapes relative to more fragmentation-sensitive species, such as Northern Long-eared Bats. Though Northern Long-eared Bats will use forest edges (Jantzen and Fenton 2013), they are far less suited to fragmented landscapes and are more commonly detected in forest interiors foraging under closed canopies (Broders et al. 2006, De La Cruz et

al. 2023, Ford et al. 2005, Henderson and Broders 2008, LaVal et al. 1977). This reliance on natural foraging habitats may constrain the ability of WNS-impacted species to persist or recover in urbanized regions, highlighting why understanding species-specific responses to urbanization remains a critical research focus.

The Chesapeake and Ohio Canal National Historical Park (CHOH) is an ideal mid-Atlantic study area for examining how bat activity relates to urbanization and habitat as it spans a diverse urban-to-rural gradient and multiple physiographic regions from Cumberland, MD, to Washington, DC. Prior to the emergence of WNS, Johnson et al. (2008) used acoustic monitoring and mist-netting in 2003–2004 to first describe bat community structure and patterns of nightly activity along this gradient within 11 National Park Service units in the National Capital Region, including CHOH. To assess changes in bat communities following the arrival of WNS in Maryland (2010–2011), Deeley et al. (2021) compared mist-netting and acoustic-sampling data from 2016–2018 with pre-WNS data collected from the same regions and reported decreases in the abundance and distribution of Little Brown Bats, Northern Long-eared Bats, and Tricolored Bats in the CHOH.

More recent research suggests that some Little Brown Bat populations may be stabilizing and even increasing in the northeastern US (Dobony and Johnson 2018, Hoyt et al. 2021, Ineson 2020, Ineson et al. 2023). Hoyt et al. (2021) conducted meta-analyses of published data from peer-reviewed papers and state and federal reports and found that the growth rate of Little Brown Bats included in these study areas was stabilizing and possibly increasing ~6 years after the introduction of WNS. A 14-year mark–recapture study at 8 maternity colonies in New England found that survival rates have stabilized and, in some cases, exceeded pre-WNS levels (Ineson 2020). Additionally, projections for 3 of these colonies, incorporating both mark–recapture and 13 years of emergence data, suggested continued growth into the future (Ineson 2020). Another study at a maternity colony on Fort Drum Military Installation in northern New York found an 88% decline in colony size between 2008 and 2010, followed by colony stabilization between 2010 and 2014, and growth after 2014 (Dobony and Johnson 2018).

Collectively, these studies indicate that stabilization and growth of Little Brown Bat populations are possible in parts of the northeastern US following severe WNS-related declines. However, it remains unclear whether colonies and/or populations in the mid-Atlantic region have followed similar recovery trajectories. Evidence of potential stabilization has also begun to emerge for the Tricolored Bat, though patterns remain regionally variable. Some Tricolored Bat colonies are now using cooler hibernacula microclimates that are less optimal for fungal growth (Johnson et al. 2016, Loeb and Winters 2022). After a loss of 90% of individuals hibernating in a cave in South Carolina after the advent of WNS, the number of Tricolored Bats hibernating in the site increased between 2018 to 2021 (Loeb and Winters 2022). Additionally, southern colonies may be buffered from mortality by the absence of WNS in the southeastern Coastal Plain, making this area a refugium for some Tricolored Bats (Shute et al. 2021). Conversely, Northern Long-eared Bats have continued their downward trajectory towards local extinction throughout much of their North American distribution (Cheng et al. 2021, Hoyt et al. 2021, USFWS 2022).

Nightly acoustic recordings offer a way to track patterns of relative activity, or the number of calls detected by an acoustic detector per night, among bat species, allowing for comparisons across ecological and temporal variables (Deeley et al. 2021). Based on differences in roosting ecology and foraging behavior, we expect these 3 species to respond differently to habitat and environmental conditions along the CHOH gradient. We hypothesized that Little Brown Bat activity may be increasing in some areas, reflecting partial recovery following WNS and their flexibility in roosting and foraging habitats. We further predicted that Little Brown Bat activity would be highest in areas with abundant forest, riparian zones, and wetlands, as well as some developed areas that can provide roosting opportunities. We hypothesized that Tricolored Bats would be associated with forests and riparian zones and could show upward trends in activity. Finally, we predicted that Northern Long-eared Bats would be associated with forest interiors and would show no change or further declines in activity, reflecting ongoing vulnerability to WNS. These predictions allowed us to test how disease history, habitat composition, and landscape development have interacted to shape species-specific patterns of relative activity. Relative-activity models for these species, derived from nightly acoustic data collected across sites and years, provided a framework to evaluate these hypotheses and inform conservation and management strategies along the CHOH and similar mid-Atlantic landscapes.

Field-Site Description

We placed acoustic detectors along a 313-km stretch of the CHOH, adjacent to the Potomac River, from Cumberland, MD, to Washington, DC (Fig. 1). The CHOH encompasses 5980 ha, ~70% of which is forested (Miller et al. 2016). Adjacent cover types to the CHOH included suburban development, livestock pastures, hayfields, and agricultural row-crops (Deeley et al. 2021). The CHOH spans 3 physiographic provinces from west to east: the Ridge and Valley, Blue Ridge Mountains, and Piedmont. The Ridge and Valley province is characterized by extensive deciduous forest cover interspersed with agricultural land, relatively low wetland availability, moderate development concentrated in valley cities, and large tracts of unfragmented forested ridges (VDCR 2021). The Blue Ridge Mountains are defined by higher elevations, steep topography, and the highest proportion of contiguous, protected forest in the region with relatively low levels of development (VCDR 2021). In contrast, the Piedmont consists of lower-relief landscapes that have been extensively altered by agriculture and urbanization, resulting in fragmented secondary forests, greater development intensity, and fewer large blocks of intact natural habitat (VCDR 2021).

Methods

Acoustic-data collection

To assess the relative activity of each bat species, we collected nightly acoustic data between May and September during 2016–2017 and 2020–2022 using

stationary SM4BAT zero-crossing/frequency division acoustic detectors equipped with SMM-UI omni-directional microphones mounted on 3-m extendable poles (Wildlife Acoustics, Maynard, MA). Detectors were programmed to record from 30 minutes before sunset until 30 minutes after sunrise and recorded for a minimum of 6 nights. We processed recorded acoustic calls using Kaleidoscope Pro software v. 5.5.0 (classifier version 5.5.0; 0 sensitivity setting; Wildlife Acoustics) following US Fish and Wildlife Service acoustic-monitoring protocols (USFWS 2023). To minimize species misidentification, we only classified files that included a minimum of 3 pulses per call file (Muthersbaugh et al. 2019). We applied USFWS survey guideline sampling-duration protocols developed for *Myotis sodalis* Miller and G.M. Allen (Indiana Bat) to survey for Little Brown Bats, Tricolored Bats, and Northern Long-eared Bats. This protocol requires a maximum likelihood estimate (MLE), or the probability of misclassification due to Type 1 error, with a threshold of $\alpha \leq 0.05$ (Ford et al. 2024, USFWS 2023). We considered species present if MLE

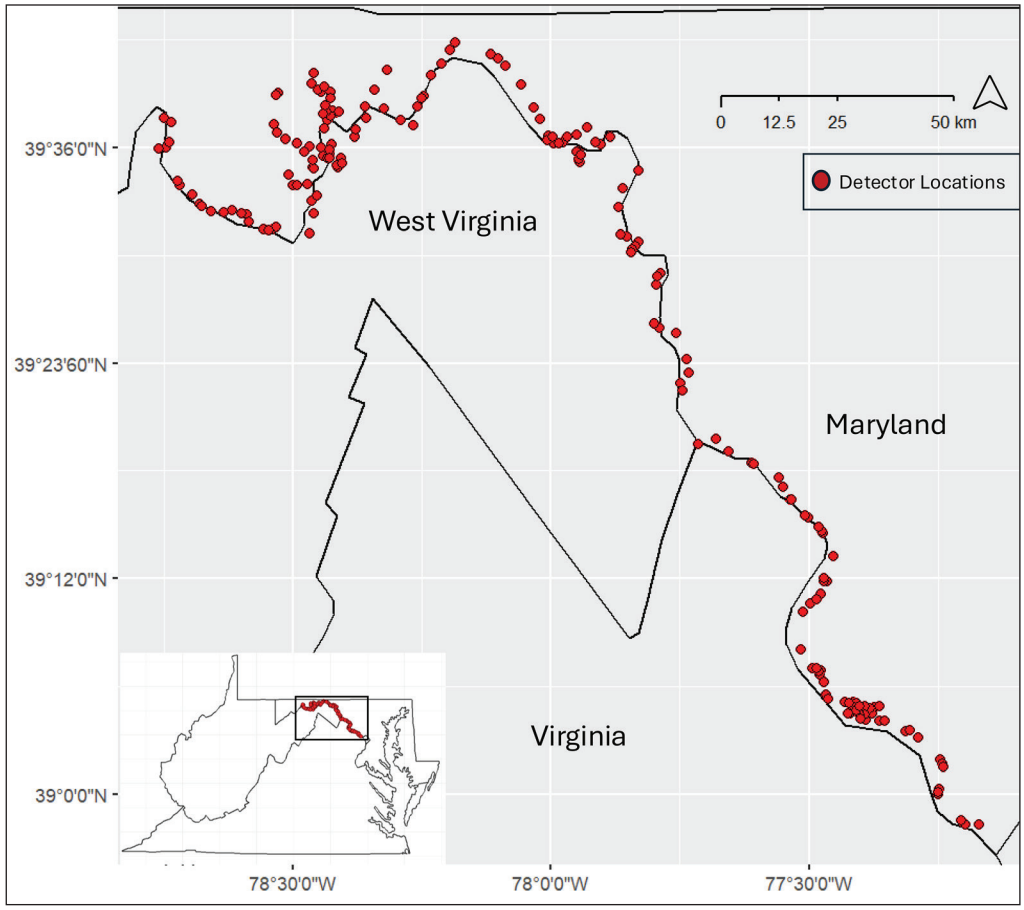

Figure 1. Map of acoustic survey locations on the Chesapeake and Ohio Canal National Historical Park, MD, during the summer of 2016–2017 and 2020–2022. We sampled 194 sites across 5 years with a total of 8776 detector nights. Detector locations are represented by red circles.

values were $P \leq 0.05$, and for values above that threshold, we considered species absent owing to potential misclassification (Ford et al. 2024).

Habitat and weather measurements

We used the following habitat variables as covariates to model bat activity response: proportion forest (deciduous, evergreen, and mixed), proportion lower development (areas characterized by parks, golf courses, and large-lot residential development with substantial vegetative cover and <50% impervious surface), proportion higher development (areas dominated by denser residential, commercial, or industrial land uses with limited vegetative cover and ≥50% impervious surface), proportion wetlands (woody and emergent), proportion open non-forested (pasture, crops, shrub, and barren), and distance to water. We obtained land-use and land-cover data from the National Land Cover Database (NLCD) 2019 raster dataset (Dewitz 2022). We incorporated proportion of each cover type into our models by calculating the percent of each type within a 500-m radius buffer of each recording station. We selected this buffer size to represent the local landscape likely influencing nightly foraging activity of Little Brown Bats, Tricolored Bats, and Northern Long-eared Bats, while minimizing overlap among sampling sites (De La Cruz et al. 2021). We also incorporated amount of daily precipitation (4-km resolution) into our analyses using data from the PRISM Climate Group (2023). Additionally, we included date and year in our models to better understand activity patterns within and among sampling years (Ford et al. 2011, Hoyt et al. 2021, O'Shea et al. 2003, Loeb and Winters 2022, Perry et al. 2010). This approach allowed us to examine finer-scale differences across individual years within the dataset. We tested all predictor variables for potential multicollinearity (threshold = |0.6|) using the 'corrplot' package v. 0.95 in R v. 4.4.1 (R Core Team 2024, Wei et al. 2017). We did not use correlated variables in the same models.

Relative-activity analysis

We examined relative bat activity in relation to habitat and weather features in our study area, by fitting a series of candidate generalized linear mixed models (GLMMs) based on a priori hypotheses, using the 'glmmTMB' package v. 1.1.10 (Brooks et al. 2017) in R. Prior to model testing, we centered and scaled all our continuous predictor variables, facilitating model fitting and interpretation, enabling direct comparison of effect sizes (Schielzeth 2010). We used a zero-inflated negative binomial generalized linear mixed model (GLMM) to account for overdispersed count data and excess zeros (Austin et al. 2018, Fournier et al. 2012). Our models consisted of 2 components: (1) a count sub-model, that models the observed counts (relative activity) assuming a negative binomial distribution, and (2) a zero-inflation sub-model to model the probability of excess zeros in the data.

We included proportional availability of forest, lower development, higher development, wetlands, open non-forested habitat, distance to water, precipitation, day of the year (ordinal date), and year as fixed effects. Proportion forest was correlated with proportion open non-forest and proportion wetland (threshold = |0.6|) and thus were not included in the same models. To account for repeated

samples at individual sites, we used detector sites as a random effect. We included the same predictor variables in the conditional and zero-inflated sub-models. We fit models based on a priori hypotheses, modeling all continuous variables with second-order polynomials to explore potential nonlinear relationships with bat activity. We conducted post hoc pairwise comparisons of year using the 'multcomp' package v. 1.4.26 (Hothorn et al. 2016) in R with Tukey's adjustment for multiple comparisons to evaluate differences between factor levels (Hothorn et al. 2016). We then compared models using Akaike's information criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002, 2004). We assessed the goodness-of-fit and over-/under-dispersion of our top model using the 'DHARMa' v. 0.4.7 (Hartig 2024) and 'stats' v. 4.4.1 (R Core Team 2024) packages in R, including a quantile–quantile plot, residual plot, and non-parametric bootstrap one-sample Kolmogorov–Smirnov (K–S) test, as traditional K–S tests often are overly conservative for zero-inflated distributions (Aldirawi et al. 2019; Lilliefors 1967, 1968; Wang et al. 2020).

Finally, we assessed spatial autocorrelation using neighborhood matrices and Moran's I of the residuals of our models (Dray et al. 2006). Using the package 'spdep' v. 1.3.6 (Bivand et al. 2013) in program R, we created a distance-based spatial weight matrix of our sites with a distance threshold of a 5-km radius. This distance encompassed reported home-range sizes of all 3 species we examined (Coleman et al. 2014, Litterer 2024, Owen et al. 2003, Thames 2020, Whitaker 1998) and ensures that each site has at least 1 neighbor (Bauman et al. 2018). Using this spatial weight matrix, we then assessed the Moran's I of the residuals of our top models to assess residual spatial autocorrelation (Dray et al. 2006).

Results

We sampled 195 sites from 2016–2017 and 2020–2022 along the CHOH resulting in a total of 8776 detector nights (Fig. 1). For both the Tricolored Bat and Northern Long-eared Bat models, the top 2 models had comparable performance ($\Delta AICc < 2$; Tables 1, 2). Given their similar results, we selected the more parsimonious model, as both identified the same significant predictors (Burnham and Anderson 2002). We did not have residual spatial autocorrelation, as the Moran's I value of the residuals of our top Little Brown Bat, Tricolored Bat, and Northern Long-eared Bat models were $P = 0.43$, $P = 0.77$, and $P = 0.51$, respectively.

The best-approximating model for Little Brown Bat relative activity on the CHOH included day of the year, precipitation, proportion wetland, distance to water, proportion lower development, and year (Table 3), which all had significant relationships to Little Brown Bat activity (Table 4). In the conditional component of the model, day of the year had a significant negative linear effect ($Z = -12.45$, $P < 0.01$) and a significant negative quadratic relationship to activity ($Z = -17.16$, $P < 0.01$). Activity increased through the early and mid-summer, with highest activity in July, and then decreased in the late summer and early fall (Fig. 2). Little Brown Bat activity had a significant negative association with precipitation amount ($Z = -3.87$, $P < 0.01$; Fig. 2), though the quadratic term was positive and significant

($Z = 2.67$, $P = 0.01$). Little Brown Bat activity had a significant positive quadratic relationship with proportion of wetlands, whereby activity dipped with lower/medium proportions, and then increased exponentially as proportion of wetlands

Table 1. Rankings of models predicting summer *Perimyotis subflavus* (Tricolored Bat) activity on the Chesapeake and Ohio Canal National Historical Park, MD, 2016–2017, 2020–2022, with k (number of parameters), Akaike's information criteria corrected (AIC_c) value corrected for small sample size, difference in AIC_c value between best supported model and i^{th} model (ΔAIC_c), and w_i (model weight).

Model	k	AICc	ΔAICc	w_i
Day + Day^2 + Precipitation + Precipitation^2 + Distance to water + Distance to water^2 + Year + (1|Site)	25	28,086.9	0.00	0.51
Day + Day^2 + Precipitation + Precipitation^2 + Distance to water + Distance to water^2 + Proportion wetland + Proportion wetland^2 + Year + (1|Site)	29	28,087.31	0.42	0.42
Day + Day^2 + Precipitation + Precipitation^2 + Proportion wetland + Proportion wetland^2 + Year + (1|Site)	21	28,091.21	4.31	0.06
Day + Day^2 + Precipitation+ Precipitation^2 + Proportion low development + Proportion low development^2 + Proportion high development + Proportion high development^2 + Proportion forest + Proportion forest^2 + Distance to water + Distance to water^2 + Year + (1|Site)	37	28,097.14	10.23	0.003
Day + Day^2 + Precipitation+ Precipitation^2 + Proportion low development + Proportion low development^2 + Proportion high development + Proportion high development^2 + Proportion open nonforest + Proportion open nonforest^2 + Proportion wetland + Proportion wetland^2 + Distance to water + Distance to water^2 + Year + (1|Site)	41	28,195.31	18.4	0.0001

Table 2. Rankings of models predicting summer *Myotis septentrionalis* (Northern Long-eared Bat) activity on the Chesapeake and Ohio Canal National Historical Park, MD, 2016–2017, 2020–2022, with k (number of parameters), Akaike's information criteria corrected (AIC_c) value corrected for small sample size, difference in AIC_c value between best supported model and i^{th} model (ΔAIC_c), and w_i (model weight).

Model	k	AICc	ΔAICc	w_i
Day + Day^2 + Proportion low development + Proportion low development^2 + Year + (1|Site)	21	7028.99	0.00	0.54
Day + Day^2 + Year + (1|Site)	17	7030.30	1.30	0.28
Day + Day^2 + Precipitation+ Precipitation^2 + Proportion low development + Proportion low development^2 + Year + (1|Site)	25	7031.29	2.30	0.17
Day + Day^2 + Precipitation+ Precipitation^2 + Proportion low development + Proportion low development^2 + Proportion high development + Proportion high development^2 + Proportion forest + Proportion forest^2 + Distance to water + Distance to water^2 + Year + (1|Site)	37	7045.87	16.87	0.0001
Day + Day^2 + Precipitation+ Precipitation^2 + Proportion low development + Proportion low development^2 + Proportion high development + Proportion high development^2 + Proportion open nonforest + Proportion open nonforest^2 + Proportion wetland + Proportion wetland^2 + Distance to water + Distance to water^2 + Year + (1|Site)	41	7051.56	22.57	0.00001

increased (Z = 2.33, P = 0.02; Table 4, Fig. 2). Lower development as a proportion of the landscape had a significant negative linear relationship (Z = -3.05, P = < 0.01) and a significant quadratic relationship with Little Brown Bat activity (Z = 2.33, P = 0.02). Relative activity significantly increased in all years compared to 2016, with the highest effect observed in 2022 (β = 1.65, Z = 6.18, P < 0.01). Post hoc pairwise comparisons revealed that Little Brown Bat activity was significantly higher in 2022 compared to all other years (P < 0.01). Activity in 2016 was significantly lower than in 2017 (Z = 3.24, P = 0.01), 2020 (Z = 3.27, P = 0.01), 2021 (Z = 3.87, P < 0.01), and 2022 (Z = 6.18, P < 0.01). However, no significant differences were observed between 2017, 2020, and 2021 (P > 0.05) (Fig. 2).

For the zero-inflation component of the Little Brown Bat model, year was a significant predictor, with the probability of excess zeros decreasing in later years (Table 4). This result indicates that Little Brown Bats were more consistently present at sites in later years: 2017 (Z = -5.66, P < 0.01), 2020 (Z = -3.91, P < 0.01), 2021 (Z = -10.76, P < 0.01), and 2022 (Z = -13.32, P < 0.01). Additionally, day of year exhibited significant effects on zero-inflation, with both the linear (Z = 6.79, P < 0.01) and quadratic terms (Z = 10.31, P < 0.01) significantly contributing to the model (Table 4). Distance to water and proportion wetland also had significant effects on zero-inflation probabilities. Distance to water had

Table 3. Rankings of models predicting summer *Myotis lucifugus* (Little Brown Bat) activity on the Chesapeake and Ohio Canal National Historical Park, MD, 2016–2017, 2020–2022, with k (number of parameters), Akaike's information criteria corrected (AIC_c) value corrected for small sample size, difference in AIC_c value between best supported model and i^{th} model (ΔAIC_c), and w_i (model weight).

Model	k	AICc	ΔAICc	w_i
Day + Day^2 + Precipitation + Precipitation^2 + Distance to water + Distance to water^2 + Proportion wetland + Proportion wetland^2 + Proportion low development + Proportion low development^2 + Year + (1|Site)	33	52310.18	0	0.63
Day + Day^2 + Precipitation + Precipitation^2 + Proportion low development + Proportion low development^2 + Distance to water + Distance to water^2 + Proportion open nonforested + Proportion open nonforested ^{2} + Proportion wetland + Proportion wetland^2 + Year + (1|Site)	37	52312.18	2.00	0.23
Day + Day^2 + Precipitation+ Precipitation^2 + Proportion low development + Proportion low development^2 + Proportion wetland + Proportion wetland^2 + Year + (1|Site)	29	52313.57	3.40	0.12
Day + Day^2 + Precipitation+ Precipitation^2 + Proportion low development + Proportion low development^2 + Proportion high development + Proportion high development^2 + Proportion open nonforest + Proportion open nonforest^2 + Proportion wetland + Proportion wetland^2 + Distance to water + Distance to water^2 + Year + (1|Site)	41	52319.03	8.85	0.001
Day + Day^2 + Precipitation+ Precipitation^2 + Proportion low development + Proportion low development^2 + Proportion high development + Proportion high development^2 + Proportion forest + Proportion forest^2 + Distance to water + Distance to water^2 + Year + (1|Site)	37	52326.52	16.35	0.0002

a positive linear relationship (Z = 2.52, P = 0.01), but a significant negative quadratic effect (Z = -2.35, P = 0.02). Proportion wetland on the landscape also had a positive linear effect (Z = 3.14, P < 0.01) and a stronger significant negative quadratic effect (Z = -3.20, P < 0.01). Lower development was not significant in the zero-inflated component of the model (Table 4).

Table 4. Predictor variables, beta coefficients (β) and standard error (SE) estimates, Z-values, and P-values of best supported model predicting nightly relative (i.e. number of nightly echolocation recordings; conditional sub-model) and probable (i.e. likelihood of zero recordings; zero-inflated model) summer activity of *Myotis lucifugus* (Little Brown Bat) on the Chesapeake and Ohio Canal National Historical Park, Maryland, 2016–2017, 2020–2022. Day and Day^2: Terms of the linear and quadratic polynomial effects of day of the year; Precipitation and Precipitation^2: Terms of the linear and polynomial quadratic effects of daily precipitation (mm); Proportion wetland and Proportion wetland^2: Terms of the linear and polynomial quadratic effects of proportion wetland within a 1km buffer of each site; Distance to water and Distance to water^2: Terms of the linear and polynomial quadratic effects of Euclidean distance to water; Proportion lower development and Proportion lower development^2: Terms of the linear and quadratic effects of proportion lower development within a 1km buffer of each site; Year 2017, Year 2020, Year 2021, Year 2022: Terms of the effects of each year as a categorical variable. * indicates statistically significant P-values.

Parameter	β	SE	Z	P(>|z|)
Conditional model				
Day	-0.20	0.02	-12.45	<0.001*
Day^2	-0.25	0.02	-17.16	<0.001*
Precipitation(mm)	-0.09	0.02	-3.87	<0.001*
Precipitation(mm)^2	0.01	0.004	2.67	0.008*
Proportion wetland	-0.33	0.19	-1.73	0.08
Proportion wetland^2	0.20	0.09	2.33	0.02*
Distance to water(m)	0.41	0.24	1.71	0.09
Distance to water(m)^2	-0.07	0.07	-0.90	0.37
Proportion lower development	-0.30	0.10	-3.05	0.002*
Proportion lower development^2	0.05	0.02	2.33	0.02*
Year2017	0.75	0.23	3.24	0.001*
Year2020	0.91	0.28	3.27	0.001*
Year2021	1.04	0.27	3.87	<0.001*
Year2022	1.65	0.27	6.18	<0.001*
Zero-inflated model				
Day	0.22	0.03	6.79	<0.001*
Day^2	0.31	0.03	10.32	<0.001*
Precipitation(mm)	0.14	0.05	2.98	0.002*
Precipitation(mm)^2	-0.02	0.01	-1.93	0.05
Proportion wetland	1.22	0.39	3.14	0.002*
Proportion wetland^2	-0.60	0.19	-3.20	0.002*
Distance to water(m)	1.23	0.49	2.52	0.01*
Distance to water(m)^2	-0.39	0.17	-2.35	0.02*
Proportion lower development	0.30	0.21	1.47	0.14
Proportion lower development^2	-0.08	0.05	-1.74	0.08
Year 2017	-1.23	0.22	-5.66	<0.001*
Year 2020	-1.25	0.32	-3.91	<0.001*
Year 2021	-3.14	0.29	-10.76	<0.001*
Year 2022	-3.96	0.30	-13.32	<0.001*

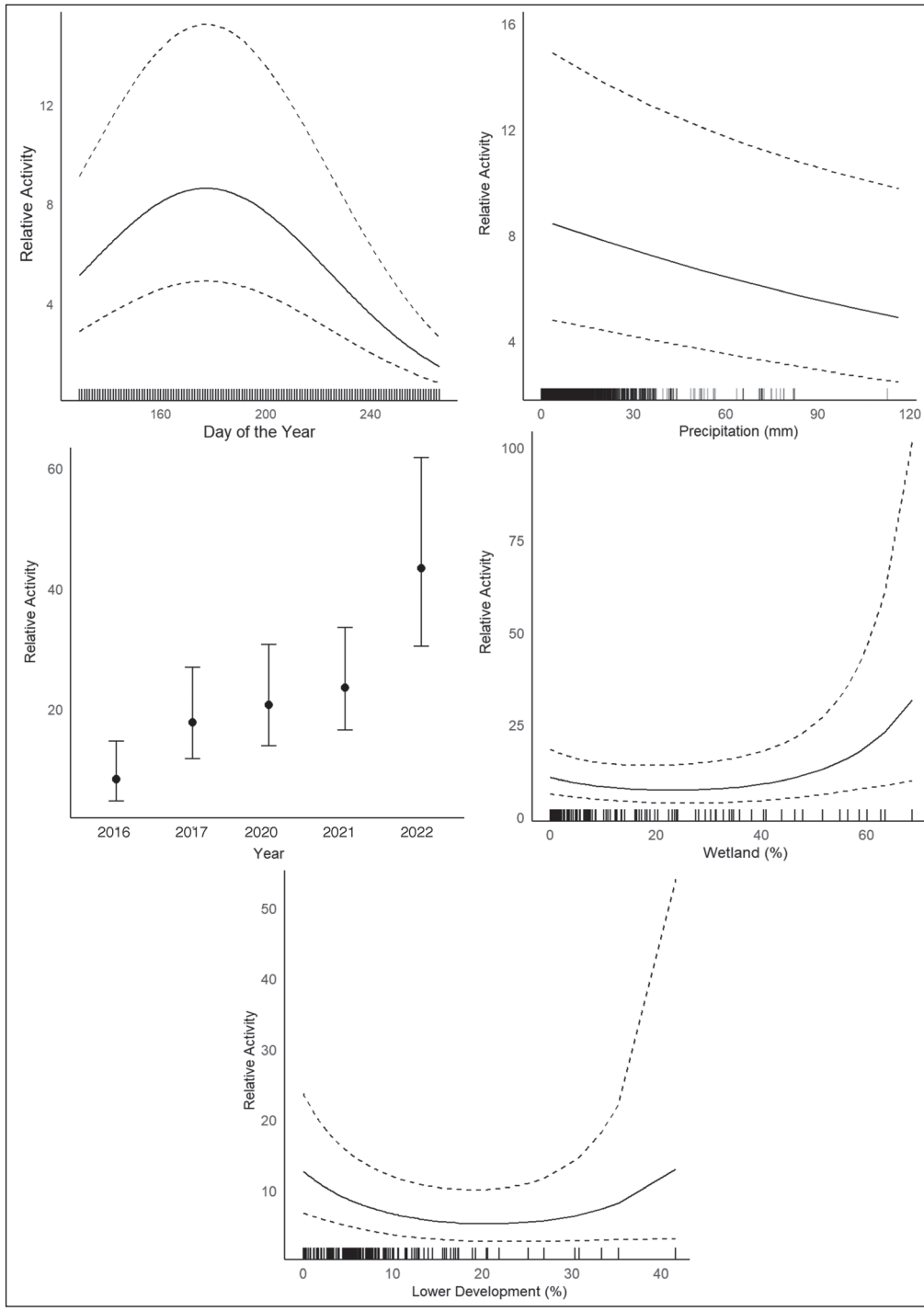

Figure 2. Partial effect plots of predicted *Myotis lucifugus* (Little Brown Bat) relative activity (number of calls per detector-night; and 95% confidence interval) for significant variables, based on data from the Chesapeake and Ohio Canal National Historical Park, MD, 2016–2017, 2016–2017, 2020–2022.

The best-approximating model for Tricolored Bat relative activity on the CHOH included day of the year, precipitation, distance to water, and year, with 1 competing model ($\Delta AIC_c < 2$; Table 1), which included the same covariates as well as proportion wetlands (Table 5). This model passed goodness-of-fit tests. In the conditional component of the model, like for Little Brown Bats, day of the year had a significant negative linear effect ($Z = -6.88$, $P < 0.01$) and a significant negative quadratic relationship to Tricolored Bat activity ($Z = -13.92$, $P < 0.01$). Activity increased through the early and mid-summer, with highest activity in July, and then decreased in the late summer and early fall (Fig. 3). Precipitation had a small, but significant, negative effect ($Z = -1.99$, $P = 0.046$), whereas its quadratic term was not significant ($Z = 0.28$, $P = 0.78$) (Table 5). Distance to water was not significant in the conditional component of our model. Post hoc Tukey comparisons indicated significant differences in activity rates among years. All years had significant differences in activity ($P < 0.01$), with greater activity in later years (Table 5, Fig. 3).

Table 5. Predictor variables, beta coefficients (β) and standard error (SE) estimates, z-values, and *P*-values of best supported model predicting nightly relative (i.e. number of nightly echolocation recordings; conditional sub-model) and probable (i.e. likelihood of zero recordings; zero-inflated model) summer activity of *Perimyotis subflavus* (Tricolored Bat) on the Chesapeake and Ohio Canal National Historical Park, MD, 2016–2017, 2020–2022. Day and Day^2: Terms of the linear and quadratic polynomial effects of day of the year; Precipitation and Precipitation^2: Terms of the linear and polynomial quadratic effects of daily precipitation (mm); Distance to water and Distance to water^2: Terms of the linear and polynomial quadratic effects of Euclidean distance to water; Year 2017, Year 2020, Year 2021, Year 2022: Terms of the effects of each year as a categorical variable. * indicates statistically significant *P*-values.

Parameter	β	SE	Z	$P(>\|z\|)$
Conditional model				
Day	-0.16	0.02	-6.88	<0.001*
Day^2	-0.29	0.02	-13.91	<0.001*
Precipitation(mm)	-0.07	0.03	-1.99	0.046*
Precipitation(mm)^2	0.002	0.01	0.28	0.78
Distance to water(m)	-0.68	0.35	-1.92	0.06
Distance to water(m)^2	0.17	0.12	1.34	0.18
Year2017	1.16	0.21	5.49	<0.001*
Year2020	2.56	0.32	8.00	<0.001*
Year2021	3.58	0.31	11.58	<0.001*
Year2022	3.58	0.31	12.73	<0.001*
Zero-inflated model				
Day	-0.12	0.03	-3.58	<0.001*
Day^2	0.19	0.03	6.00	<0.001*
Precipitation	0.03	0.05	0.57	0.57
Precipitation^2	0.01	0.01	0.91	0.37
Distance to water	1.08	0.43	2.53	0.01*
Distance to water^2	-0.29	0.15	-1.96	0.05*
Year 2017	-0.22	0.21	-1.04	0.30*
Year 2020	1.33	0.33	3.97	<0.001*
Year 2021	0.06	0.30	0.21	0.84
Year 2022	-0.07	0.31	-0.21	0.83

In the zero-inflation component of the Tricolored Bat model, year had a significant increase in zero-inflation for 2020 ($Z = 3.97$, $P < 0.01$) but no significant effects for other years (Table 5). Day of the year had a negative linear effect ($Z = -3.58$, $P < 0.001$), while its quadratic term had a positive effect ($Z = 5.99$, $P < 0.01$). Distance to water was positively significant ($Z = 2.53$, $P = 0.01$), whereas its quadratic term showed a marginal negative effect ($Z = -1.96$, $P = 0.05$). Precipitation was not significant in the zero-inflation component (Table 5).

The best-approximating model for Northern Long-eared Bat relative activity on the CHOH included day of the year and year (Table 2). This model passed goodness-of-fit tests. A competing model (ΔAICc < 2) also included proportion lower development in the landscape, though it was not a significant predictor. In the

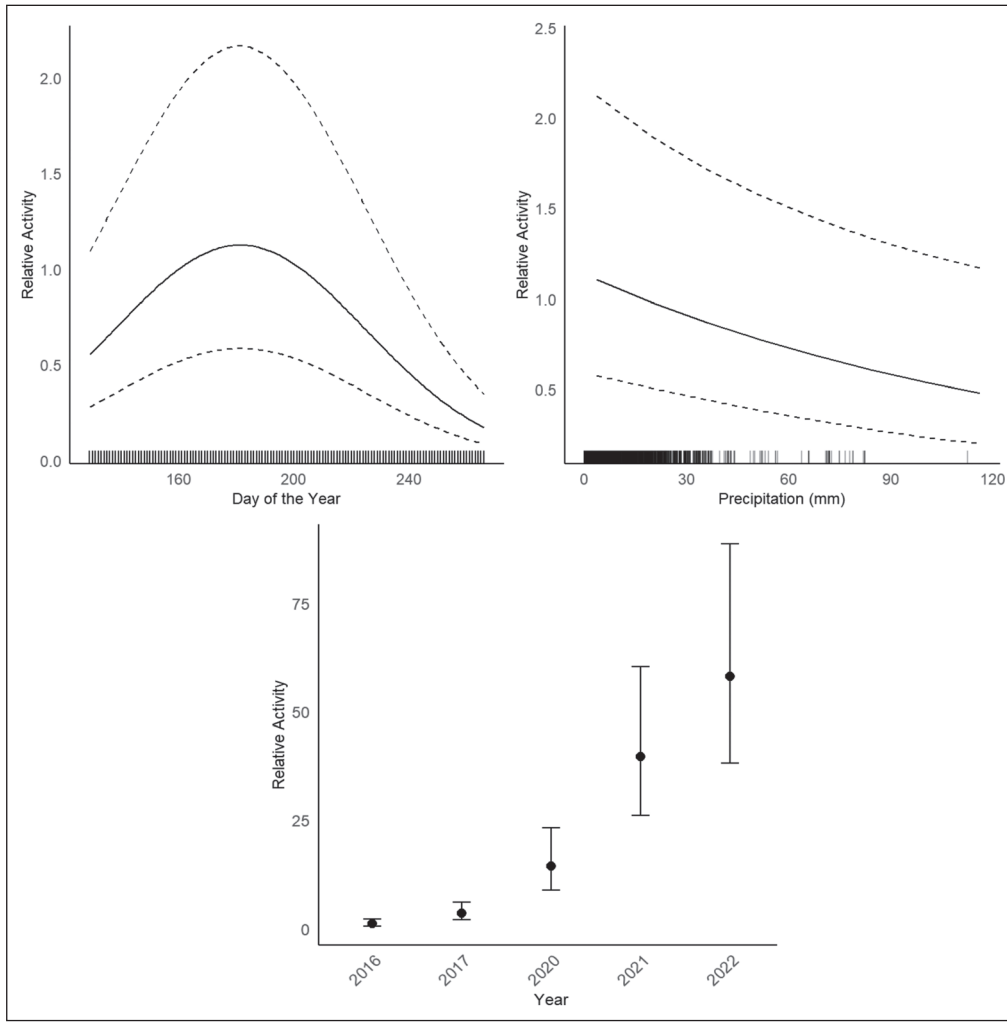

Figure 3. Partial effect plots of predicted *Perimyotis subflavus* (Tricolored Bat) relative activity (number of calls per detector-night; and 95% confidence interval) for significant variables, based on data from the Chesapeake and Ohio Canal National Historical Park, MD, 2016–2017, 2020–2022.

conditional component of our model, day of the year and year had significant associations with activity (Table 6). The linear effect of day of the year was positively significant (Z = 2.27, P = 0.02) for Northern Long-eared Bats, but unlike for Little Brown and Tricolored bats, the quadratic term was non-significant (Z = -0.04, P =

Table 6. Predictor variables, beta coefficients (β) and standard error (SE), z-values, and P-values of best supported model predicting nightly relative (i.e. number of nightly echolocation recordings; conditional sub-model) and probable (i.e. likelihood of zero recordings; zero-inflated model) summer activity of *Myotis septentrionalis* (Northern Long-eared Bat) on the Chesapeake and Ohio Canal National Historical Park, MD, 2016–2017, 2020–2022. Day and Day^2: Terms of the linear and quadratic polynomial effects of day of the year; Year 2017, Year 2020, Year 2021, Year 2022: Terms of the effects of each year as a categorical variable. * indicates statistically significant P-values.

Parameter	β	SE	Z	P(>|z|)
Conditional model				
Day	0.10	0.04	2.27	0.02*
Day^2	-0.002	0.04	-0.04	0.96
Year2017	0.44	0.68	0.65	0.52
Year2020	1.31	0.66	2.00	0.05*
Year2021	2.37	0.61	3.89	<0.001*
Year2022	2.71	0.61	4.42	<0.001*
Zero-inflated model				
Day	-0.02	0.05	-0.56	0.58
Day^2	-0.21	0.05	-4.54	<0.001*
Year 2017	0.67	0.59	1.13	0.26
Year 2020	0.18	0.62	0.29	0.78
Year 2021	-0.84	0.59	-1.44	0.15
Year 2022	-0.46	0.59	-0.78	0.44

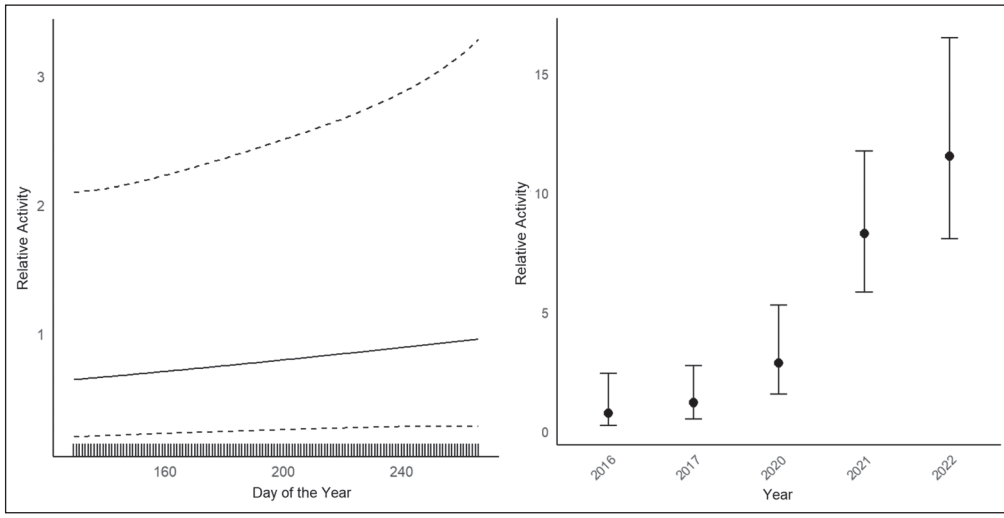

Figure 4. Partial effect plots of predicted *Myotis septentrionalis* (Northern Long-eared Bat) relative activity (number of calls per detector-night; and 95% confidence interval) for significant variables, based on data from the Chesapeake and Ohio Canal National Historical Park, MD, 2016–2017, 2020–2022.

0.96) (Table 6, Fig. 4). There were significant differences in Northern Long-eared Bat activity among years, with post-hoc Tukey comparisons indicating activity in 2021 and 2022 was significantly higher than in 2016 ($Z = 3.89$, $P < 0.01$; $Z = 4.42$, $P < 0.01$, respectively) and 2017 ($Z = 4.44$, $P < 0.01$; $Z = 5.18$, $P < 0.01$, respectively). Additionally, 2021 had a significantly higher detection rate than 2020 ($Z = 3.24$, $P < 0.01$), and 2022 had a significantly higher detection rate than both 2020 ($Z = 4.27$, $P < 0.01$) and 2021 ($Z = 3.53$, $P < 0.01$). However, there were no significant differences between 2017 and 2016 ($Z = 0.65$, $P = 0.96$) or between 2020 and 2016 ($Z = 2.00$, $P = 0.23$). Similarly, 2020 and 2017 did not differ significantly ($Z = 1.82$, $P = 0.32$; Table 6, Fig. 4).

For the zero-inflated component of the Northern Long-eared bat model, the quadratic term for day was negative and significant ($Z = -4.54$, $P < 0.01$), suggesting that low activity was most common in early spring and late fall, with the lowest probability of zeros occurring in mid-summer. However, year effects were non-significant, indicating that the probability of zero inflation did not differ across years (Table 6).

Discussion

Our results indicate that, following severe declines associated with WNS, relative activity of Little Brown and Tricolored Bats along the CHOH has increased in recent years. Consistent with our predictions, relative activity of Little Brown Bat increased significantly in 2021 and 2022 compared to 2016, suggesting increased use of the landscape or greater nightly activity at monitored sites. These patterns are consistent with reports of stabilization in some northeastern populations (Dobony and Johnson 2018, Hoyt et al. 2021, Ineson et al. 2023), and though these patterns alone cannot confirm population recovery, they may indicate as much. Additionally, as there is the chance populations could exhibit a cyclical pattern of increases followed by decreases due to density-dependent transmission of *Pd*, whereby larger colonies could lead to greater *Pd* spread and mortality from WNS (Langwig et al. 2012), continued monitoring might be beneficial to verify continued population growth into the future.

Similar to Little Brown Bats on the CHOH during this time period, Tricolored Bats exhibited increasing activity across years. There is evidence of persistence and even slight population increases in more southern regions of Tricolored Bat distribution (Loeb and Winters 2022). Factors contributing to this trend may include the use of culvert and transportation structures as hibernacula, which may offer more stable temperatures and less suitable substrate to support *Pd* (Andersen et al. 2022, Grider et al. 2021, Newman et al. 2021). Moreover, hibernation periods along portions of the CHOH may be shorter than those found in the Northeast or the more mountainous adjacent portions of the Ridge and Valley and Appalachian Plateau (Boyles et al. 2020, Dunbar and Brigham 2010, Wolbert et al. 2014).

Northern Long-eared Bat activity also appears to be increasing in later years, with 2021 and 2022 exhibiting significantly more activity than preceding years. However, it is important to note that Northern Long-eared Bats site-night acoustic

observations overall were very low, with ~6% of sites detecting this species per night and an overall mean relative activity of 0.90. In contrast, Little Brown Bats were detected on 50% of site-nights with a mean relative activity of 34.26, and Tricolored Bats were detected on 25% of site-nights with a mean relative activity of 12.67. These low detection rates suggest that even seemingly large proportional increases in the number of recorded calls could represent very small absolute changes, limiting the biological relevance of such trends. For example, doubling in activity could result in an increase from just 1 to 2 echolocation calls on a nightly basis. This change would still be exceedingly low and would not indicate a meaningful population trend, particularly for a species that prior to WNS was among the most common bats in the region (Deeley et al. 2021). Although not indicative of population growth over time, this increase in all species activity in 2021 may reflect a higher recruitment year, possibly due in part to the 17-year periodical *Magicicada* spp. (cicada) emergence cylce. The Brood X emergence may have either enhanced survival of remaining bats or attracted individuals from non-cicada areas into the existing population (Litterer 2024). Based on guano analyses, Little Brown Bats, which are of similar size to Northern Long-eared Bats, have been confirmed to feed on cicadas (Isenhour et al. 2024). The emergence provides a pulse of large, energy-rich prey that is easily captured (Maier 1982), which may have led to local immigration, higher pup survival, and improved body condition of bats entering hibernation.

Relative activity of Little Brown Bats increased from late spring to early summer, peaking in late June. As observed from other research, this period of greater activity aligns with influx of newly volant bats when the pups begin foraging on the landscape (Fenton and Barclay 1980, Ford et al. 2011). Patterns of relative activity of Tricolored Bats were similar, with the highest activity in early July. Relative activity of Northern Long-eared Bats was lowest in the early portion of the summer survey period and gradually increased into late summer and fall. This pattern may be driven by juvenile recruitment during the maternity season, but if local maternity colonies failed, as reported in the Central Appalachian Mountains (Francl et al. 2012, Kalen et al. 2022), it could also reflect early dispersal of surviving individuals to nearby hibernacula. This pattern of low Northern Long-eared Bat activity led to a lack of significance for the quadratic effect of day in the conditional component of our model. However, the zero-inflated component of the Northern Long-eared Bat model suggests that excess non-detection nights were most common during the early and later portions of our survey seasons. Accordingly, from this analytical perspective, the seasonal trend for the Northern Long-eared Bat is similar to that of the Little Brown Bat and Tricolored Bat.

Unsurprisingly, both Little Brown Bat and Tricolored Bat activity was negatively associated with precipitation, as foraging decreases during periods of precipitation on the surrounding landscape (Patriquin et al. 2016, Smith and McWilliams 2016). The habitat associations identified in our models also have been supported by previous research (Fenton and Barclay 1980). Proportion of wetlands was significant in both components of the Little Brown Bat model, with activity initially decreasing at lower to moderate levels of wetland coverage but then increasing exponentially

as the proportion of wetlands rises, which is consistent with the quadratic trend in the zero-inflated component, where the likelihood of zero events increases at lower wetland proportions but decreases at higher proportions. Though distance to water was not significant in the conditional component of the model, there was a similar trend to wetlands in the zero-inflated component of the model. Although distance to water did not strongly influence activity at sites where Little Brown Bats were present, it was an important predictor of whether bats were detected at all. Specifically, the probability of zero detections was lowest at intermediate distances from water, suggesting a unimodal relationship. This result suggests that water availability primarily affects site use rather than activity intensity, highlighting an optimal range of distances where bats are most likely to occur. These findings align with previous work showing that water is a key resource for foraging and commuting bats (Coleman and Barclay 2011, Ford et al. 2005, Litterer 2024, Menzel et al. 2005, Nocera et al. 2020, Zimmerman and Glanz 2000), but uniquely, our results demonstrate an intermediate optimum rather than a simple linear effect. Little Brown Bat relative activity also decreases with increasing amounts of lower development, but then begins to increase again, as explained by negative linear and positive quadratic relationship between proportion lower development and activity. Little Brown Bats are commonly associated with both rural and suburban areas (Fenton and Barclay 1980, Coleman et al. 2014, Litterer 2024, Nocera et al. 2020, Zimmerman and Glanz 2000), possibly due to abundance of anthropogenic structures for day-roosting (Coleman and Barclay 2011, Davis and Hitchcock 1965, Frick et al. 2010, Olson and Barclay 2013, Reimer et al. 2016). This pattern may reflect nightly activity patterns, roosting in less developed rural areas (with structures) and foraging in riparian areas and wetlands with little development nearby (Coleman and Barclay 2011, Fenton and Barclay 1980). Relative activity patterns of Tricolored Bats were similar to those of Little Brown Bat with their relationship with distance to water. Though not significant in the conditional component of the model, the results of the zero-inflated component suggest that as distance to water increases, so does the probability of zero detections. Tricolored Bats were more likely to be detected at sites closer to water. Similar to Little Brown Bats, Tricolored Bats tend to forage close to, or above water and are commonly associated with riparian habitat (Cable and Willcox 2024, Ford et al. 2005, Leput 2004, Menzel et al. 2005, O'Keefe et al. 2009, Veilleux et al. 2003).

Overall, our findings underscore the importance of wetland habitats and proximity to water for Little Brown Bats and Tricolored Bats, aligning with their known habitat use. Because the CHOH National Historical Park provides a protected corridor of these habitats along the Potomac River, it represents an important resource for these species, particularly in the context of an increasingly changing landscape due in part to continued development and urbanization along the Potomac River corridor, particularly eastward towards the Washington, DC, metropolitan area (Dewitz 2022, USFWS 2011). The observed increases in Little Brown Bat and Tricolored Bat activity in recent years may reflect changes in bat use of the area and recovery; however, confirming actual population changes will

ultimately require actual counts of bats through roost surveys or capture–recapture studies. The persistence of these species may reflect localized adaptations or temporary environmental shifts favoring their survival. Conversely, relative activity of Northern Long-eared Bats in our study area remains low and is consistent with broader declines observed in other studies (Cheng et al. 2021, Hoyt et al. 2021, Hyzy et al. 2020, Perea et al. 2024). Continuous research and monitoring would be needed to understand the long-term impacts of environmental changes and conservation efforts on these bat populations.

Acknowledgments

Special thanks to Andrew Landsman and staff from the Chesapeake and Ohio Canal National Historical Park that assisted with study coordination. Project funding was provided by the National Park Service Chesapeake Cooperative Ecosystem Study Unit grant P19AC01216 to Virginia Tech. Any use of trade, firm, or product names in this manuscript is for descriptive purposes only and does not imply endorsement by the US Government. At the time of publication, data were not publicly available from the National Park Service. M.L. Moran (mlmoran@vt.edu) can be contacted for data availability.

Literature Cited

Aldirawi, H., J. Yang, and A.A. Metwally. 2019. Identifying appropriate probabilistic models for sparse discrete omics data. Institute of Electrical and Electronics Engineers Engineering in Medicine and Biology Society International Conference on Biomedical and Health Informatics. Chicago, IL. 4 pp.

Andersen, B.R., L.P McGuire, T.B. Wigley, D.A. Miller, and R.D. Stevens. 2022. Habitat associations of overwintering bats in managed pine forest landscapes. Forests 13(5):article 803.

Austin, L.V., A. Silvis, W.M. Ford, M. Muthersbaugh, and K.E. Powers. 2018. Bat activity following restoration prescribed burning in the central Appalachian upland and riparian habitats. Natural Areas Journal 38(2):183–195.

Bauman, D., T. Drouet, M.J. Fortin, and S. Dray. 2018. Optimizing the choice of a spatial weighting matrix in eigenvector-based methods. Ecology 99(10):2159–2166.

Bivand, R., E. Pebesma, and V. Gómez-Rubio. 2013. Applied Spatial Data Analysis with R. Second Edition. Springer, New York, NY. 405 pp.

Blehert, D.S., A.C. Hicks, M. Behr, C.U. Meteyer, B.M. Berlowski-Zier, E.L. Buckles, J.T. Coleman, S.R. Darling, A. Gargas, R. Niver, and J.C. Okoniewski. 2009. Bat white-nose syndrome: An emerging fungal pathogen? Science 323(5911):227–227 .

Boyles, J.G., J.S. Johnson, A. Blomberg, and T.M. Lilley. 2020. Optimal hibernation theory. Mammal Review 50(1):91–100.

Bradley, C.A., and S. Altizer. 2007. Urbanization and the ecology of wildlife diseases. Trends in Ecology and Evolution 22(2):95–102.

Broders, H.G., G.J. Forbes, S. Woodley, and I.D. Thompson. 2006. Range extent and stand selection for roosting and foraging in forest-dwelling Northern Long-eared Bats and Little Brown Bats in the Greater Fundy ecosystem, New Brunswick. Journal of Wildlife Management 70(5):1174–1184.

Brooks, M.E., K. Kristensen, K.J. Van Benthem, A. Magnusson, C.W. Berg, A. Nielsen, H.J. Skaug, M. Machler, and B.M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9(2):378–400.

Brooks, R.T. 2011. Declines in summer bat activity in central New England 4 years following the initial detection of white-nose syndrome. Biodiversity and Conservation 20:2537–2541.

Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Inference: A Practical Information-Theoretic Approach. 2nd Edition, Springer-Verlag, New York, NY. 353 pp.

Burnham, K.P., and D.R. Anderson. 2004. Multimodel inference: Understanding AIC and BIC in model selection. Sociological Methods and Research 33(2):261–304.

Cable, A.B., and E.V. Willcox. 2024. Summer habitat for the female Tricolored Bat (*Perimyotis subflavus*) in Tennessee, United States. Journal of Mammalogy 105(3):667–678.

Cheng, T.L., J.D. Reichard, J.T. Coleman, T.J. Weller, W.E. Thogmartin, B.E. Reichert, A.B. Bennett, H.G. Broders, J. Campbell, K. Etchison, and D.J. Feller. 2021. The scope and severity of white-nose syndrome on hibernating bats in North America. Conservation Biology 35(5):1586–1597.

Coleman, J.L., and R.M. Barclay. 2011. Influence of urbanization on demography of Little Brown Bats (*Myotis lucifugus*) in the prairies of North America. PLoS ONE 6(5):article e20483.

Coleman, L.S., W.M. Ford, C.A. Dobony, and E.R. Britzke. 2014. Comparison of radiotelemetric home-range analysis and acoustic detection for Little Brown Bat habitat evaluation. Northeastern Naturalist 21(3):431– 445.

Davis, W.H., and H.B. Hitchcock. 1965. Biology and migration of the bat *Myotis lucifugus* in New England. Journal of Mammalogy 46(2):296–313.

De La Cruz, J.L. 2024. Spatial ecology and conservation strategies for the endangered Northern Long-eared Bat (*Myotis septentrionalis*) in a post-white-nose syndrome landscape. Ph.D. Dissertation. Virginia Tech, Blacksburg, VA. 148 pp.

De La Cruz, J.L., C. Stearns, and S. Webb. 2021. Stationary acoustic bat survey report and recommendations for the Maine Department of Inland Fisheries and Wildlife. Project Final Report for Contract # CT-09A-20240221*2273. Virginia Tech, Blacksburg, VA. 41 pp.

De La Cruz, J.L., W.M. Ford, S. Jones, J.B. Johnson, and A. Silvis. 2023. Distribution of Northern Long-eared Bat summer habitat on the Monongahela National Forest, West Virginia. Journal of the Southeastern Association of Fish and Wildlife Agencies 10:114–124.

Deeley, S., J.B. Johnson, W.M. Ford, and J.E. Gates. 2021. White-nose syndrome related changes to Mid-Atlantic bat communities across an urban-to-rural gradient. BMC Zoology 6(1):article 12.

Dewitz, J. 2022. National land cover database (NLCD) 2021. (version 2.0). US Geological Survey Data Release. Available online at https://doi.org/10.5066/P9KZCM54. Accessed 14 March 2024

Dobony, C.A., and J.B. Johnson. 2018. Observed resiliency of Little Brown Myotis to long-term white-nose syndrome exposure. Journal of Fish and Wildlife Management 9(1):168–179.

Dray, S., P. Legendre, and P.R. Peres-Neto. 2006. Spatial modelling: A comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecological Modelling 196:483−493.

Duchamp, J.E., and R.K. Swihart. 2008. Shifts in bat community structure related to evolved traits and features of human-altered landscapes. Landscape Ecology 23:849–860.

Dunbar, M.B., and R.M. Brigham. 2010. Thermoregulatory variation among populations of bats along a latitudinal gradient. Journal of Comparative Physiology B 180:885–893.

Fenton, M.B., and R.M. Barclay. 1980. *Myotis lucifugus*. Mammalian species (142):1–8.

Ford, W.M., M.A. Menzel, J.L. Rodrigue, J.M. Menzel, and J.B. Johnson. 2005. Relating bat species presence to simple habitat measures in a central Appalachian forest. Biological Conservation 126(4):528–539.

Ford, W.M., E.R. Britzke, C.A. Dobony, J.L. Rodrigue, and J.B. Johnson. 2011. Patterns of acoustical activity of bats prior to and following white-nose syndrome occurrence. Journal of Fish and Wildlife Management 2(2):125–134.

Ford, W.M., J.L. De La Cruz, E.D. Thorne, A. Silvis, M.P. Armstrong, and R.A. King. 2024. Second guessing the maximum likelihood estimator values for bat surveys. Journal of the Southeastern Association of Fish and Wildlife Agencies 11:177–184.

Fournier, D.A., H.J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M.N. Maunder, A. Nielsen, and J. Sibert. 2012. AD model builder: Using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software 27:233−249.

Francl, K.E., W.M. Ford, D.W. Sparks, and V. Brack Jr. 2012. Capture and reproductive trends in summer bat communities in West Virginia: Assessing the impact of white-nose syndrome. Journal of Fish and Wildlife Management 3(1):33–42.

Frick, W.F., J.F. Pollock, A.C. Hicks, K.E. Langwig, D.S. Reynolds, G.G. Turner, C.M. Butchkoski, and T.H. Kunz. 2010. An emerging disease causes regional population collapse of a common North American bat species. Science 329(5992):679–682.

Gaisler, J., J. Zukal, Z. Rehak, and M. Homolka. 1998. Habitat preference and flight activity of bats in a city. Journal of Zoology 244(3):439–445.

Gargas, A., M.T. Trest, M. Christensen, T.J. Volk, and D.S. Blehert. 2009. *Geomyces destructans* sp. nov. associated with bat white-nose syndrome. Mycotaxon 108(1):147–154.

Grider, J.F., R.E. Russell, A.E. Ballmann, and T.J. Hefley. 2021. Long-term *Pseudogymnoascus destructans* surveillance data reveal factors contributing to pathogen presence. Ecosphere 12(11):article e03808.

Hartig, F. 2024. DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4.7. R Foundation for Statistical Computing, Vienna, Austria. Available online at https://cran.r-project.org/package=DHARMa. Accessed 14 March 2024

Henderson, L.E., and H.G. Broders. 2008. Movements and resource selection of the Northern Long-eared Myotis (*Myotis septentrionalis*) in a forest–agriculture landscape. Journal of Mammalogy 89(4):952–963.

Hothorn, T., F. Bretz, P. Westfall, R.M. Heiberger, A. Schuetzenmeister, S. Scheibe, and M.T. Hothorn. 2016. Package 'multcomp': Simultaneous inference in general parametric models. R package version 1.4.26. Project for Statistical Computing, Vienna, Austria. Available online at https://cran.r-project.org/package=multcomp. Accessed 14 March 2024

Hoyt, J.R., A.M. Kilpatrick, and K.E. Langwig. 2021. Ecology and impacts of white-nose syndrome on bats. Nature Reviews Microbiology 19(3):196–210.

Hyzy, B.A., R.E. Russell, A. Silvis, W.M. Ford, J. Riddle, and K. Russell. 2020. Occupancy and detectability of Northern Long-eared Bats in the Lake States region. Wildlife Society Bulletin 44(4):732–740.

Ineson, K.M. 2020. Demography of a recovery: tracking the rebound of Little Brown Bat (*Myotis lucifugus*) populations. Ph.D. Dissertation. University of New Hampshire, Durham, NH. 159 pp.

Ineson, K.M., C.S. Richardson, C.E. Looney, N.W. Fuller, and J.D. Reichard. 2023. Patterns of post-hibernation wing damage healing in Little Brown Bats (*Myotis lucifugus*) impacted by white-nose syndrome. Journal of Mammalogy 104:1072–1083.

Isenhour, Z., G.L. Harris, R.L. Stewart, E.D. Hampton, M.R. Scafini, G.G. Turner, and S.E. Bergsten. 2024. Dietary flexibility of insectivorous bats, *Eptesicus fuscus* and *Myotis lucifugus*, during *Magicicada* spp. Brood X emergence. Canadian Journal of Zoology 102(11):888–895.

Jachowski, D.S., C.A. Dobony, L.S. Coleman, W.M. Ford, E.R. Britzke, and J.L. Rodrigue. 2014. Disease and community structure: White-nose syndrome alters spatial and temporal niche partitioning in sympatric bat species. Diversity and Distributions 20(9):1002–1015.

Jantzen, M.K., and M.B. Fenton. 2013. The depth of edge influence among insectivorous bats at forest–field interfaces. Canadian Journal of Zoology 91(5):287–292.

Johnson, J.B., J.E. Gates, and W.M. Ford. 2008. Distribution and activity of bats at local and landscape scales within a rural–urban gradient. Urban Ecosystems 11:227–242.

Johnson, J.S., M.R. Scafini, B.J. Sewall, and G.G. Turner. 2016. Hibernating bat species in Pennsylvania use colder winter habitats following the arrival of white-nose syndrome. Pp. 181–199, *In* C.M. Butchkowski, D.A.M. Reeder and G.G. Turner (Eds.). Conservation and Ecology of Pennsylvania's Bats. The Pennsylvania Academy of Science, Philadelphia,PA. 267 pp.

Jung, K., C.G. and Threlfall. 2016. Urbanisation and its effects on bats—A global meta-analysis. Pp. 13–33, *In* C.C. Voigt and T. Kingston (Eds.). Bats in the Anthropocene: Conservation of Bats in a Changing World Springer, Springer Nature, Cham, Switzerland. 606 pp.

Kalen, N.J., M.S. Muthersbaugh, J.B. Johnson, A. Silvis, and W.M. Ford. 2022. Northern Long-eared Bats in the central Appalachians following white-nose syndrome: Failed maternity colonies. Journal of the Southeastern Association of Fish and Wildlife Agencies 9:159–167.

Kurta, A., and J.A. Teramino. 1992. Bat community structure in an urban park. Ecography 15(3):257–261.

Langwig, K.E., W.F. Frick, J.T. Bried, A.C. Hicks, T.H. Kunz, and M.A. Kilpatrick. 2012. Sociality, density-dependence and microclimates determine the persistence of populations suffering from a novel fungal disease, white-nose syndrome. Ecology Letters 15(9):1050–1057.

LaVal, R.K., R.L. Clawson, M.L. LaVal, and W. Caire. 1977. Foraging behavior and nocturnal activity patterns of Missouri bats, with emphasis on the endangered species *Myotis grisescens* and *Myotis sodalis*. Journal of Mammalogy 58:592–599.

Leput, D.W., 2004. Eastern Red Bat (*Lasiurus borealis*) and Eastern Pipistrelle (*Pipistrellus subflavus*) maternal roost selection: implications for forest management. M.Sc. Thesis. Clemson University, Clemson, SC. 89 pp.

Lilliefors, H.W. 1967. On the Kolmogorov–Smirnov test for normality with mean and variance unknown. Journal of the American statistical Association 62(318):399–402.

Lilliefors, H.W. 1968. Elements of nonparametric statistics (Gottfried E. Noether). Society for Industrial and Applied Mathematics Review 10(3):394–396.

Litterer, A.S. 2024. Bat resource utilization along the Potomac River corridor in Maryland. M.Sc. Thesis. Virginia Tech, Blacksburg, VA. 71 pp.

Loeb, S.C., and J.M. O'Keefe. 2006. Habitat use by forest bats in South Carolina in relation to local, stand, and landscape characteristics. Journal of Wildlife Management70(5):1210–1218.

Loeb, S.C., and E.A. Winters. 2022. Changes in hibernating Tricolored Bat (*Perimyotis subflavus*) roosting behavior in response to white-nose syndrome. Ecology and Evolution 12(7):article e9045.

Loeb, S.C., C.J. Post, and S.T. Hall. 2009. Relationship between urbanization and bat community structure in national parks of the southeastern US. Urban Ecosystems 12:197–214.

Lorch, J.M., C.U. Meteyer, M.J. Behr, J.G. Boyles, P.M. Cryan, A.C. Hicks, A.E. Ballmann, J.T. Coleman, D.N. Redell, D.M. Reeder, and D.S. Blehert. 2011. Experimental infection of bats with *Geomyces destructans* causes white-nose syndrome. Nature 480(7377):376–378.

Maier, C.T. 1982. Observations on the seventeen-year periodical cicada, *Magicicada septendecim* (Hemiptera: Homoptera: Cicadidae). Annals of the Entomological Society of America 75:17–23.

Menzel, J.M., M.A. Menzel Jr, J.C. Kilgo, W.M. Ford, J.W. Edwards, and G.F. McCracken. 2005. Effect of habitat and foraging height on bat activity in the coastal plain of South Carolina. Journal of Wildlife Management 69(1):235–245.

Miller, K.M., F.W. Dieffenbach, J.P. Campbell, W.B. Cass, J.A. Comiskey, E.R. Matthews, B.J. McGill, B.R. Mitchell, S.J. Perles, S. Sanders, J.P. Schmit, S. Smith, and A.S. Weed. 2016. National parks in the eastern United States harbor important older forest structure compared with matrix forests. Ecosphere 7(7):1–20.

Muthersbaugh, M.S., W.M. Ford, K.E. Powers, and A. Silvis. 2019. Activity patterns of bats during the fall and spring along ridgelines in the central Appalachians. Journal of Fish and Wildlife Management 10(1):180–195.

Newman, B.A., S.C. Loeb, and D.S. Jachowski. 2021. Winter roosting ecology of Tricolored Bats (*Perimyotis subflavus*) in trees and bridges. Journal of Mammalogy 102:1331–1341.

Nocera, T., W.M. Ford, C. Dobony, and A. Silvis. 2020. Temporal and spatial changes in *Myotis lucifugus* acoustic activity before and after white-nose syndrome on Fort Drum Army Installation, New York, USA. Acta Chiropterologica 22(1):121–134.

O'Keefe J.M., S.C. Loeb, J.D. Lanham, and H.S. Hill. 2009. Macrohabitat factors affect day roost selection by Eastern Red Bats and Eastern Pipistrelles in the southern Appalachian Mountains, USA. Forest Ecology and Management 257:1757–1763.

Olson, C.R., and R.M. Barclay. 2013. Concurrent changes in group size and roost use by reproductive female Little Brown Bats (*Myotis lucifugus*). Canadian Journal of Zoology 91(3):149–155.

O'Shea, T.J., M.A. Bogan, and L.E. Ellison. 2003. Monitoring trends in bat populations of the United States and territories: Status of the science and recommendations for the future. Wildlife Society Bulletin 31:16–29.

Owen, S.F., M.A. Menzel, W.M. Ford, B.R. Chapman, K.V. Miller, J.W. Edwards, and P.B. Wood. 2003. Home-range size and habitat used by the Northern Myotis (*Myotis septentrionalis*). American Midland Naturalist 150(2):352–359.

Patriquin, K.J., M.L. Leonard, H.G. Broders, W.M. Ford, E.R. Britzke, and A. Silvis. 2016. Weather as a proximate explanation for fission–fusion dynamics in female Northern Long-eared Bats. Animal Behaviour 122:47–57.

Perea, S., E.A. Ferrall, K.M. Morris, P.E. Pattavina, N. Sharp, and S.B. Castleberry. 2024. A decade of hibernating bat communities along the periphery of a region of white-nose syndrome. Journal of Wildlife Management 88(1):article e22506.

Perry, R.W., S.A. Carter, and R.E. Thill. 2010. Temporal patterns in capture rate and sex ratio of forest bats in Arkansas. American Midland Naturalist 164(2):270–282.

PRISM Climate Group. 2023. PRISM climate data. Data created 28 December 2023. Oregon State University, Corvallis, OR. Available online at https://prism.oregonstate.edu. Accessed 28 December 2023.

R Core Team. 2024. R: A language and environment for statistical computing. Version 4.4.1. R Foundation for Statistical Computing, Vienna, Austria. Available online at https://www.R-project.org. Accessed 14 March 2024

Reimer, J.P., L.A. Kaupas, and P.A. Schuette. 2016. Little Brown Myotis maternity-roost surveys: Copper River basin, 2016.Alaska Center for Conseration Science, University of Alaska, Juneau, AK. 23 pp.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution 1(2):103–113.

Schimpp, S.A., H. Li, and M.C. Kalcounis-Rueppell. 2018. Determining species-specific nightly bat activity in sites with varying urban intensity. Urban Ecosystems 21:541–550.

Shute, K.E., S.C. Loeb, and D.S. Jachowski. 2021. Summer roosting ecology of the Northern Yellow Bat and Tri-colored Bat in coastal South Carolina. Southeastern Naturalist 20(3):459–476.

Smith, A.D., and S.R. McWilliams. 2016. Bat activity during autumn relates to atmospheric conditions: Implications for coastal wind energy development. Journal of Mammalogy 97(6):1565–1577.

Straw, B.R., J.A. Martin, J.D. Reichard, and B.E. Reichert. 2022. Analytical assessments in support of the US Fish and Wildlife Service 3-bat species status assessment. Cooperator Report prepared in cooperation with the US Geological Survey, US Fish and Wildlife Service, and Bat Conservation International. Ft. Collins, CO. 78 pp.

Thames, D.B. 2020. Summer foraging range and diurnal roost selection of Tri-colored Bats, *Perimyotis subflavus.* M.Sc. Thesis. University of Tennessee, Knoxville, TN. 87 pp.

True, M.C., R.W. Perry, and W.M. Ford. 2021. Forecasting the distribution of a range-expanding bat reveals future response to climate change and habitat. Acta Chiropterologica 23(1):139–152.

US Fish and Wildlife Service (USFWS). 2011. Status and trends of wetlands in the conterminous United States 2004 to 2009. 107 pp. Available online at https://www.fws.gov/sites/default/files/documents/Status-and-Trends-of-Wetlands-in-the-Conterminous-United-States-2004-to-2009.pdf. Accessed 14 March 2024.

USFWS. 2022. Endangered and threatened wildlife and plants; endangered species status for Northern Long-eared Bat. Federal Register 87:16442–16452

USFWS. 2023. Range-wide Indiana Bat and Northern Long-eared Bat survey guidelines. Available online at https://www.fws.gov/media/range-wide-indiana-bat-and-northern-long-eared-bat-survey-guidelines. Accessed 14 March 2024.

Veilleux, J.P., J.O. Whitaker, S.L. Veilleux. 2003. Tree-roosting ecology of reproductive female Eastern Pipistrelles, *Pipistrellus subflavus*, in Indiana. Journal of Mammalogy 84:1068–1075.

Virginia Department of Conservation and Recreation, Division of Natural Heritage (VDCR). 2021. Overview of the physiography and vegetation of Virginia. Version 2.0. Virginia Department of Conservation and Recreation, Richmond, VA. 52 pp.

Wang, L., H. Aldirawi, and J. Yang. 2020. Identifying zero-inflated distributions with a new R package iZID. Communications in Information and Systems 20(1): 23–44.

Warnecke, L., J.M. Turner, T.K. Bollinger, J.M. Lorch, V. Misra, P.M. Cryan, G. Wibbelt, D.S. Blehert, and C.K. Willis. 2012. Inoculation of bats with European *Geomyces destructans* supports the novel pathogen hypothesis for the origin of white-nose syndrome. Proceedings of the National Academy of Sciences 109(18):6999–7003.

Wei, T., V. Simko, M. Levy, Y. Xie, Y. Jin, and J. Zemla. 2017. Package 'corrplot': Visualization of a correlation matrix. R package version 0.95. R Foundation for Statistical Computing, Vienna, Austria. Available online at https://cran.r-project.org/package= corrplot. Accessed 14 March 2024

Whitaker, J.O., Jr. 1998. Life history and roost switching in six summer colonies of Eastern Pipistrelles in buildings. Journal of Mammalogy 79 (2):651–659.
Wolbert, S.J., A.S. Zellner, and H.P. Whidden. 2014. Bat activity, insect biomass, and temperature along an elevational gradient. Northeastern Naturalist 21(1):72–85.
Zimmerman, G.S., and W.E. Glanz. 2000. Habitat use by bats in eastern Maine. Journal of Wildlife Management 64(4):1032–1040.

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Source: Northeastern Naturalist, 33(1) : 104-127

Published By: Eagle Hill Institute

URL: https://doi.org/10.1656/045.033.0110