Sources of Yearly Variation in Gray Bat Activity in the Clinch River Watershed, Virginia

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Abstract: The gray bat (*Myotis grisescens*) is a cave-obligate species that has been listed as federally endangered since 1976, following population declines from human disturbance at hibernation and maternity caves. However, with cave protection, most gray bat populations have increased. As part of a project examining bat use of transportation structures as day-roosts, we continuously acoustically monitored 12 riparian sites within the Clinch River Watershed of southwest Virginia from March through November, 2018–2020. We used 15 different landscape and weather-related variables in generalized linear mixed models to determine factors influencing gray bat presence and activity. Seasonal activity patterns were similar among years, but the number of nightly gray bat calls increased with each passing year, consistent with positive population trends observed at winter hibernacula. Year and average nightly temperatures were positively correlated with gray bat activity, as was, unexpectedly, average nightly wind speed. Total nightly precipitation, distance to the nearest hibernaculum in Tennessee, percent forested area within 2 km of a detector, mean elevation within 2 km of a detector, detector type, and amount of urban development within 2 km of a detector were negatively correlated with gray bat activity. Our findings show where and when gray bat presence is likely in southwest Virginia, thereby helping managers avoid negative impacts from activities such as bridge repair or replacement and planning of future monitoring to track population trends.

Key words: acoustics, *Myotis grisescens*, landscape, weather effects

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The gray bat (*Myotis grisescens*) has been listed as endangered under the U.S. Endangered Species Act since 1976, after populations were reduced due to anthropogenic disturbances at summer and winter caves (Tuttle 1979). Unlike many cave-dwelling bat species, gray bats seem largely unaffected by *Pseudogymnoascus destructans*, the fungal pathogen that causes White-nose Syndrome (WNS; Wibbelt et al. 2010, Bernard et al. 2015, Powers et al. 2016). The population appears to be stable or increasing due to fungal resistance, potential niche release from declines in competing species, such as the little brown bat (*Myotis lucifugus*), and long-term protection of caves (Jachowski et al. 2014, Powers et al. 2015, Powers et al. 2016).

During non-hibernating months gray bats day-roost in caves or cave-like structures and forage over large streams and rivers in the mid-South and lower Midwest. The northeastern-most summer range extends into the upper Tennessee River Basin of southwest Virginia (Tuttle 1979, Keeley and Tuttle 1999, Chapman et al. 2007). There is high interest in more detailed understanding of gray bat distribution and relative abundance as they day-roost or night-roost in transportation structures, such as bridges (Keeley and Tuttle 1999, Johnson et al. 2002, Powers et al. 2016). Preliminary work in the Clinch–Powell river system in southwestern Virginia suggested that gray bat activity is concentrated within the Clinch and Powell watersheds in proximity to a hibernaculum in Hawkins County, Tennessee, and a maternity roost in Bristol on the Virginia–Tennessee border (Taylor et al. 2022).

Preceding WNS, presence of listed bat species was confirmed via mist-netting. However, with population declines of many species and subsequent low detection probability via mist-netting (Nocera et al. 2019a, Deeley et al. 2021), the United States Fish and Wildlife Service (USFWS) developed acoustic monitoring protocols for the Indiana bat (*Myotis sodalis*) and northern long-eared bat (*Myotis septentrionalis*) to guide regulatory assessment (Armstrong et al. 2022). Acoustic monitoring offers a cost-effective

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method to determine the local bat species assemblage and identify foraging habitat (Ford et al. 2005, Ford et al. 2016). Long-term acoustic sampling in multiple locations can also provide insights on seasonal and landscape variation in activity patterns (Johnson et al. 2010a, Johnson et al. 2010b, Nocera et al. 2020, Gorman et al. 2021, Taylor et al. 2022). With broader determinations of landscape-level distribution and abundance managers can assess risk both spatially and temporally beyond where survey work occurs (Barr et al. 2021). Long-term acoustics monitoring surveys pre- and post-WNS have revealed the relationship between average activity levels and relative population size for many bat species (Jachowski et al. 2014, Nocera et al. 2019b).

In 2018, we began a multi-year assessment of gray bat activity in the Clinch River portion of the upper Tennessee River watershed to better understand relationships of activity to landscape and weather covariates and to assess year-to-year variation in activity to inform monitoring needs for the Virginia Department of Transportation (VDOT). Because gray bats are summer cave-obligates that forage along river systems, we predicted that many landscape-level covariates important to other bat species, such as forest coverage, developed land, etc., would show equivocal relationships, whereas relationships to weather variables would be similar to the responses of other bat species. Furthermore, owing to the nearby presence of the gray bat maternity colony and winter hibernacula in Tennessee, we expected that seasonal patterns of activity would be related to proximity to the maternity colony from late spring through summer and to the hibernacula in fall.

Methods

Acoustic Monitoring

We selected sites based on VDOT's interest in a series of bridges along the Clinch River and tributaries in the Ridge and Valley and Appalachian Plateau (Cumberland Mountains section) physiographic provinces. Generally, along the Clinch River, the Ridge and Valley is characterized by forested mountains with moderate to steep side-slopes and broad valleys cleared for pasture and hay production (Kniowski and Ford 2018). The Appalachian Plateau is >90% forested and is characterized by steep slopes and narrow, sheltered valleys (Kniowski and Ford 2018). At each site, we placed a SM-4 zero-crossing/frequency division acoustic detector with an SMM-U1 omni-directional microphone (Wildlife Acoustics, Maynard, Massachusetts) along watercourses near bridges, as described by Coleman et al. (2014) and Austin et al. (2018). However, for five of our sites in 2020, we deployed a SM-4 full-spectrum detector provided by the Tennessee Valley Authority for use in the region (sites 00, 02, 03, 04, and 05; Figure 1). We mounted microphones on 3-m poles above vegetative clutter. At each survey site, we operated detectors continuously two hours before sunset to two hours after sunrise from March to November 2018–2020. For detector settings, we used signal detection parameters of 8–120 kilohertz (kHz) minimum and maximum frequency range and 2–500 milliseconds (ms) minimum and maximum length of detected pulses. We processed downloaded acoustic call files using the USFWS and the U.S. Geological Survey (USGS)-approved Kaleidoscope version 5.1, classifier version 1.5.9 (Wildlife Acoustics, Maynard, Massachusetts) for species-specific identification with default signal parameters (two pulse minimum and maximum inter-syllable gap of 500 ms). We set the possible species presence for the area as: Virginia big-eared bat (*Corynorhinus townsendii virginianus*), big brown bat (*Eptesicus fuscus*), eastern red bat (*Lasiurus borealis*), hoary bat (*Lasiurus cinereus*), silver-haired bat (*Lasionycteris noctivagans*), gray bat, eastern small-footed bat (*Myotis leibii*), little brown bat, northern long-eared bat, Indiana bat, and tricolored bat (*Perimyotis subflavus*). At the site level, we visually confirmed that at least one call was classified as gray bat based on sonogram shape and frequency characteristics matching those in our call library. We accepted nightly counts of all individual call files identified as gray bat irrespective of the nightly maximum likelihood estimator scores for the watershed-wide monthly activity level modeling (Nocera et al. 2020).

Statistical Analysis

We used the sum of nightly gray bat call files as our response variable and evaluated 15 candidate covariates derived from landscape or nightly weather variables. The predictor variables we evaluated for our models included site (used as a random effect), latitude, distance to nearest known significant hibernaculum, and distance to nearest known maternity colony. We identified stream order for each bridge site as an approximation of stream width using the National Hydrography Dataset layer (U.S. Environmental Protection Agency 2019) in ArcGIS Pro (Esri, Inc., Redlands, California). Because our detectors were placed along stream banks, we did not consider distance to stream as a predictor. To determine surrounding landcover types, we used The Nature Conservancy's Terrestrial Habitat Map for the Northeast U.S. (Ferree and Anderson 2015). We combined all deciduous, conifer, and mixed forest type categories into a 'forest' category. We also combined shrub/scrub, herbaceous, hay/pasture, and cultivated crops categories into a 'low vegetation' category, and low, medium, and high intensity development categories into one 'developed' category. We used ArcGIS Pro to calculate percentage of these landcover categories within a 2-km radius of each detector. To calculate the mean cave density within a 2-km radius of each detector, we used the Appalachian Landscape Conservation Cooperative's (ALCC) dataset of known caves within 20-km^2

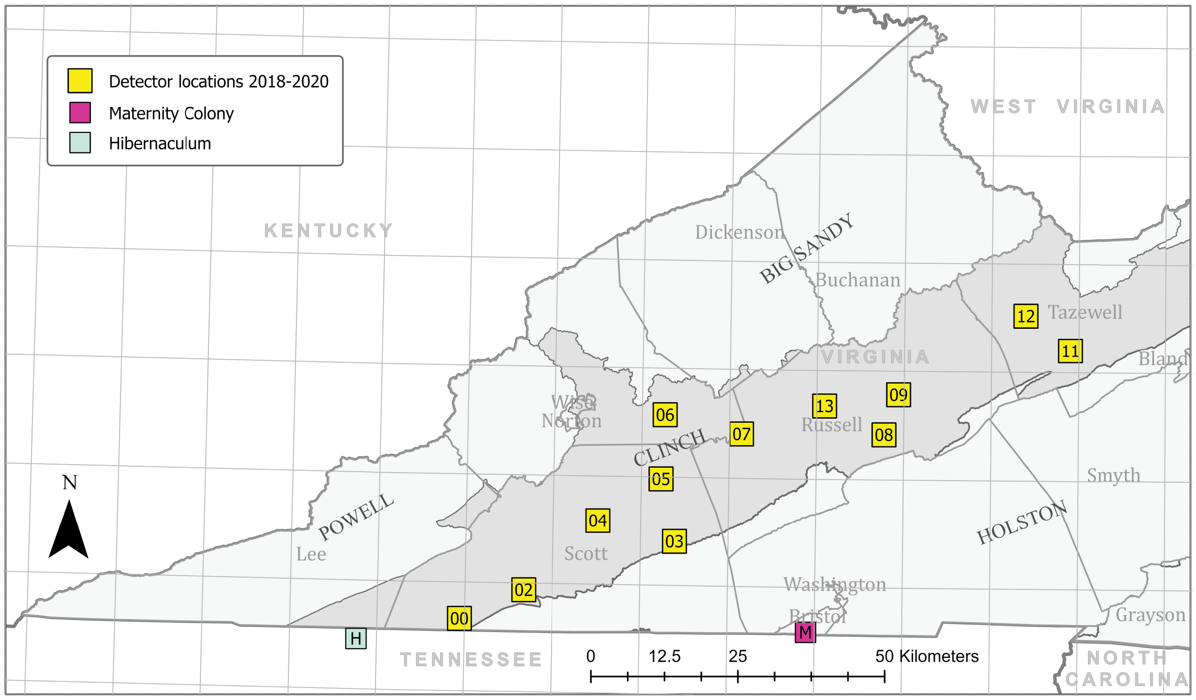

Figure 1. Known gray bat maternity colony roost, nearest known hibernaculum, and acoustic survey locations (numbers within survey location markers refer to site ID) surveyed in the Clinch River Watershed from March to November in 2018–2020.

grid cells (Doctor et al. 2016). We assumed that caves occurred only within areas defined as karst by a USGS karst data layer (Weary and Doctor 2014). We then merged the karst layer with the ALCC's 20-km^2 grid maps layer and calculated mean cave density of each karst portion of a grid cell by dividing the number of caves in the grid cell by the portion of karst area within the grid cell and averaged the mean cave density values that fell within a 2-km radius buffer around each detector. We calculated the minimum, maximum, and mean elevation (m) within a 2-km radius buffer around each detector in ArcGIS Pro using the U.S. Geological Survey (2020) layer. To determine total nightly precipitation (mm), average nightly windspeed (kmph), and average nightly temperature (C), we acquired weather data from nearest local weather stations through the METeorological Aerodrome Reports (METARs) for the dates in which our detectors were operating (Iowa Environmental Mesonet 2020). We also used the year (2018, 2019, and 2020) as a predicting variable, and the day of year (or Julian day), which we transformed by taking the cosine of radians creating a circular variable (i.e., day 1 follows day 365). Finally, to help account for and quantify the effect on detection resulting from the change in equipment type at five of our sites in 2020, we added a detector type predictor (full-spectrum versus zero-crossing).

We tested for correlation among candidate predictor variables using the corrplot package in R (R Core Team 2020, Wei and Simko 2021) and determined any variable correlations < |0.6| as acceptable. Variable pairs that exceeded the limit bounds were not combined in a model. We centered and scaled continuous variables. We ran 47 generalized linear mixed models with negative binomial distributions and log link functions including single-variable models, several *a priori* multi-variable models, and a null (no covariate) model using the lme4 package in R (Bates et al. 2015, Jorge et al. 2021). We ranked the models based on the Akaike Information Criterion for small sample sizes (AICc), and we considered models within 2 ΔAICc units as competing top models (Mazerolle 2020, Jorge et al. 2021). Using competing models, we calculated model-averaged predictions using AICc weights (Burnham and Anderson 2002).

Results

We recorded bat activity at all 12 sites, 2018–2022. We amassed 2483 detector nights between 3 April and 3 November in 2018, 2498 detector nights between 10 March and 8 November in 2019, and 2488 detector nights between 6 March and 19 November in 2020. Gray bats comprised 24.2% (403,106) of the total call files (1,668,245) identified to species. We found an increasing number of gray bat calls each year: 52,438 in 2018, 96,897 in 2019, and 253,744 in 2020 (Table 1). We also detected the remaining 11 species expected for the area (Table 1).

We had five competitive models explaining variation in gray bat call counts (Table 2). The fifth-ranked model was the only competing model to include stream order and mean cave density (Table 2),

Table 1. Number of bat calls recorded in the Clinch River Watershed, southwest Virginia from March to November in 2018–2020 by species and year across all 12 surveyed sites.

Species	2018	2019	2020
Virginia big-eared bat (*Corynorhinus townsendii virginianus*)	74	173	798
Big brown bat (*Eptesicus fuscus*)	26,953	43,189	84,886
Eastern red bat (*Lasiurus borealis*)	1426	3523	9573
Hoary bat (*Lasiurus cinereus*)	24,827	15,779	71,236
Silver-haired bat (*Lasionycteris noctivagans*)	99,120	122,859	79,241
Gray bat (*Myotis grisescens*)	52,435	96,897	253,774
Small-footed bat (*Myotis leibii*)	72	220	107
Little brown bat (*Myotis lucifugus*)	14,098	19,247	46,333
Northern long-eared bat (*Myotis septentrionalis*)	206	378	192
Indiana bat (*Myotis sodalis*)	547	10,498	2829
Evening bat (*Nycticeius humeralis*)	3992	9171	18,662
Tricolored bat (*Perimyotis subflavus*)	113,695	178,477	312,817

Table 2. Model comparisons of candidate generalized linear mixed models predicting gray bat acoustic activity from 12 sites in the Clinch River Watershed, southwest Virginia from March to November in 2018–2020. Included are model parameters for each model, the number of parameters (K), the difference in each model's Akaike's Information Criterion (with correction for small sample size, AICc) and the AICc score of the top-ranking model (ΔAICc), AICc weight (Wt), and the model log-likelihood (LL). Other than the intercept-only model, results for models with Wt <0.01 are omitted.

Model Parameters[a]	K	ΔAICc	Wt	LL
hib, forest, mean-elv, year, tmp, rain, wind, Jul, DT	12	0.00	0.19	−24,581.73
hib, forest, dev, year, tmp, rain, wind, Jul, DT	12	0.41	0.15	−24,581.94
hib, dev, year, tmp, rain, wind, Jul, DT	11	0.47	0.15	−24,582.97
hib, mean-elv, year, tmp, rain, wind, Jul, DT	11	0.94	0.12	−24,583.21
hib, MCD, forest, dev, mean-elv, year, tmp, rain, wind, SO, Jul, DT	15	1.77	0.08	−24,579.60
hib, MCD, year, tmp, rain, wind, Jul, DT	11	2.46	0.05	−24,583.97
hib, MCD, forest, year, tmp, rain, wind, Jul, DT	12	2.65	0.05	−24,583.06
hib, MCD, forest, mean-elv, year, tmp, rain, wind, SO, Jul, DT	14	2.76	0.05	−24,581.11
hib, mat, MCD, forest, dev, mean-elv, year, tmp, rain, wind, SO, Jul, DT	16	2.81	0.05	−24,579.12
hib, karst, forest, mean-elv, year, tmp, rain, wind, SO, Jul, DT	14	2.84	0.05	−24,581.15
hib, MCD, forest, year, tmp, rain, wind, SO, Jul, DT	13	3.87	0.03	−24,582.66
hib, mat, karst, forest, mean-elv, year, tmp, rain, wind, SO, Jul, DT	15	4.34	0.02	−24,580.89
year, tmp, rain, wind, Jul, DT	9	4.81	0.02	−24,587.15
forest, year, tmp, rain, wind, Jul, DT	10	6.72	0.01	−24,587.10
Intercept only	3	1066.28	0.00	−25,123.89

a. Parameters include DT: detector type (zero-crossing or full spectrum); Jul: Julian day; hib: distance to the nearest known hibernaculum (km); mat: distance to the nearest known maternity colony (km); tmp: average nightly temperature (C); rain: total nightly precipitation (cm); wind: average nightly wind speed (kmph); SO: stream order. Parameters within a 2-km radius include forest: % forested area; MCD: mean cave density; max-elv: maximum elevation (m); mean-elv: mean elevation (m); dev: % developed area; karst: % karst; two additional variables examined but not included in models shown include % area with low vegetation and minimum elevation.

both of which had $P > 0.05$, and this model had weight < 0.10. Therefore, we model-averaged predictions only from the top four models. Other predictors were significant in the competitive models (except for percent developed area ($P \geq 0.07$), mean elevation ($P \geq 0.05$), and percent forested area ($P \geq 0.07$). Average nightly temperature, average nightly windspeed, and year had positive relationships to gray bat activity (Figure 2, Figure 3). Distance from hibernaculum, total nightly precipitation, percent developed area,

Table 3. Individual parameter estimates (β) from the four top-ranking models predicting gray bat acoustic activity using data collected from 12 sites in the Clinch River Watershed, southwest Virginia from March to November in 2018–2020.

	Model 1		Model 2		Model 3		Model 4	
Parameter[a]	β	SE	β	SE	β	SE	β	SE
Intercept	3.34	0.28	3.37	0.28	3.38	0.3	3.36	0.3
DT	−1.76	0.11	−1.76	0.11	−1.76	0.11	−1.76	0.11
wind	0.08	0.03	0.08	0.03	0.08	0.03	0.08	0.03
rain	−0.11	0.03	−0.11	0.03	−0.11	0.03	−0.11	0.03
tmp	0.61	0.04	0.61	0.04	0.61	0.04	0.61	0.04
hib	−1.05	0.26	−0.8	0.27	−0.59	0.25	−0.79	0.25
year	0.26	0.05	0.26	0.05	0.26	0.05	0.26	0.05
Jul	−1.06	0.08	−1.06	0.08	−1.05	0.08	−1.05	0.08
forest	−0.47	0.26	−0.39	0.26	–	–	–	–
elv	−0.43	0.22	–	–	–	–	−0.37	0.25
dev	–	–	−0.42	0.23	−0.42	0.25	–	–

a. Parameters include DT: detector type; wind: average nightly windspeed (kmph); rain: total nightly precipitation (cm); tmp: average temperature (C); hib: distance to hibernaculum (km); forest: % forested area within a 2-km radius; Jul: Julian day; elv: average elevation within a 2-km radius; dev: % developed area within a 2-km radius.

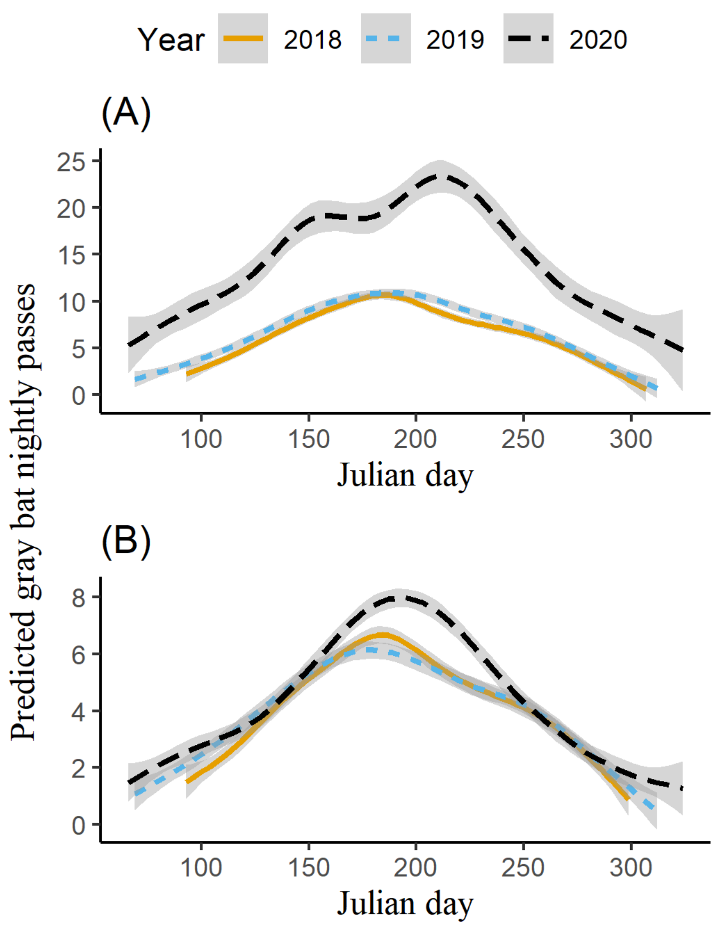

Figure 2. Model-averaged predicted nightly gray bat acoustic activity from sites within the Clinch River Watershed surveyed from March to November in 2018–2020 by Julian day and year. (A) 12 sites including five locations that had full spectrum detectors in 2020. (B) only including the seven sites within the Clinch River Watershed that had zero-crossing detectors.

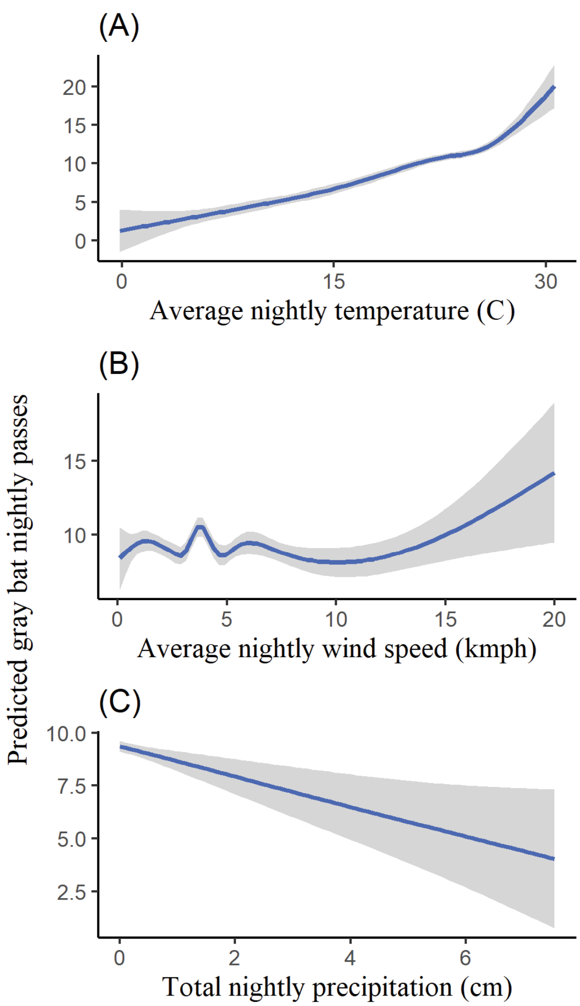

Figure 3. Model-averaged predicted nightly gray bat acoustic activity from the Clinch River Watershed from 12 sites surveyed from March to November in 2018–2020 with respect to weather variables. (A) average nightly temperature (degrees C), (B) average nightly windspeed (kmph), and (C) total nightly precipitation (mm).

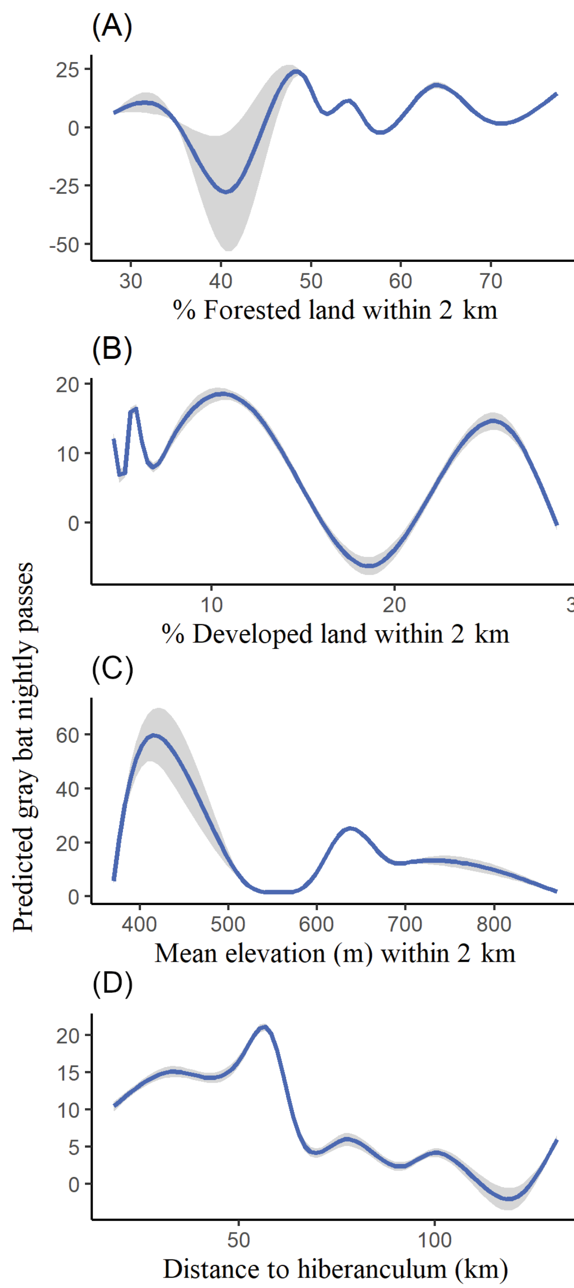

Figure 4. Model-averaged predicted nightly gray bat acoustic activity from the Clinch River Watershed from 12 sites surveyed from March to November in 2018–2020 with respect to landscape variables. (A) Percent forested-area within 2-km radius, (B) Percent developed-area within 2-km radius, (C) mean elevation within 2-km radius, and (D) distance (km) to nearest known hibernaculum in Tennessee.

mean elevation, percent forested area, detector type, and Julian day had negative relationships to gray bat activity (Figure 2, Figure 4). Of the 11 variables included in competing models, detector type, Julian day, distance to hibernaculum, and nightly temperature had stronger effects (≥ | 0.61 |; Table 3).

Discussion

Gray bat seasonal activity patterns were similar between years, yet activity increased across years. This was expected due to the benefits of cave protection, apparent resistance to WNS, and possibly niche release from competing WNS-impacted bat species (Powers et al. 2015, 2016). Assuming no major changes to habitat quality or presence of new unknown maternity caves, we believe the three-fold increase from 2018 to 2020 cannot be solely attributable to population growth, based on hibernacula counts. Although Indiana and northern long-eared bats did not show an increase over time, WNS-impacted little brown bats and tricolored bats did. This increase may be attributable to the full-spectrum detectors deployed at five sites in 2020 (sites 00–05; Figure 1). Compared to zero-crossing detectors full-spectrum detectors have higher sensitivity and produce higher quality call recordings, potentially allowing detection of more calls and enabling software to identify more passes to species-level (Adams et al. 2012; E. Barr, USFWS, Marietta, Ohio, unpublished data). Considering these five survey locations were central to the largest gray bat aggregation in the region between the maternity site, bachelor caves, and the hibernaculum, an increase in recording sensitivity may have provided inflated detection numbers. Still, gray bat activity predictions for the seven sites with zero-crossing detectors in all three years also showed a pattern of yearly activity increases, though not as extreme as the sites with full spectrum detectors (Figure 2).

The negative relationship of activity to nightly precipitation and positive relationship to temperature were expected. Bat activity across most species has been shown to increase with warmer temperatures and decrease with increasing rainfall, likely paralleling insect activity (Whitaker and Rissler 1992, Cryan and Brown 2007, Ruczyński and Bartoń 2020, Gorman et al. 2021). Bat activity is typically negatively related to windspeed (Smith and McWilliams 2016, Muthersbaugh et al. 2019). We were surprised to find a positive relationship between gray bat activity and windspeed in our models. However, weather data were derived for the general area rather than our detector sites, hence windspeed may not have been accurately characterized where we surveyed for gray bats as many of the riparian corridors were sheltered by adjacent mountains. Thus, gray bats might concentrate foraging to narrow river corridors during high wind conditions.

A negative relationship of gray bat activity to distance from the hibernaculum was expected. Powers et al. (2016) found that most gray bat summer colonies in Virginia are bachelor colonies. In the Clinch River Watershed, with potentially abundant resources (including caves), males may not forage far from their bachelor caves, as observed in northwest Georgia (Johnson et al. 2010b). Our data provide no clear evidence for seasonal dispersion within the Clinch River Watershed. However, on a larger geographic scale, across three additional watersheds, temporal and spatial variation of gray bat activity is notable with a northward flow in spring and a southern ebb in fall (Taylor et al. 2022).

To confirm the extent of gray bat population growth, methods such as multi-year exit hibernacula counts and surveys for additional, undocumented bachelor caves or maternity sites could be employed (O'Shea and Bogan 2003, Powers et al. 2016, Orndorff et al. 2019). Taylor et al. (2022) observed gray bats beyond their presumed range in the New River Watershed in 2019 and 2020 in Virginia, providing additional evidence of a growing population. This population growth may be linked to community effects of WNS, whereby the pressures of niche partitioning are relaxed for non-susceptible species (Jachowski et al. 2014, Powers et al. 2015, Bombaci et al. 2021). Beyond potential population growth and spatial range expansion, our study suggests that additional work exploring trends related to changing climate patterns relative to the onset of presence in the spring and the cessation of activity in the fall could be beneficial. A better understanding of the duration of presence and resulting risk to bats at transportation structures and contributory landscape and weather factors for potential gray bat day-roost or night-roost usage could help agencies such as VDOT minimize potential harm from maintenance or replacement actions.

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