

PREDICTORS OF BAT SPECIES OCCUPANCY ON THE  
BLUE RIDGE PARKWAY

A Thesis  
by  
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## ABSTRACT

### PREDICTORS OF BAT SPECIES OCCUPANCY ON THE BLUE RIDGE PARKWAY

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North American bat populations are facing severe pressure from anthropogenic change, land cover alterations and the white-nose syndrome epidemic. With several once-flourishing species now believed to be nearing extinction, it is important to monitor population trends and to identify foraging habitats with the aim of conserving and prioritizing preferred habitat types. This study examined bat species occupancy ( $\psi$ ) along the North Carolina portion of the Blue Ridge Parkway during the summer of 2021, where 7 of 14 species are susceptible to white-nose syndrome. Through the use of passive acoustic surveys and call identification technology, I detected 12 of the 14 species historically present. I identified biotic and abiotic factors that influence occupancy and detectability including: elevation, distance to water, percent forested land cover and weather parameters. Occupancy predictions coincided with overall species population trends in the region; protected and rare species generally exhibited lower occupancy estimates compared to more wide-spread species. Four federally endangered species (Virginia big-eared bat (*Corynorhinus townsendii virginianus*), gray bat (*Myotis grisescens*), northern long-eared bat (*Myotis septentrionalis*), and Indiana bat (*Myotis sodalis*) had relatively low estimates of occupancy ( $\psi$  range: 0.23 - 0.44) and occurred more often in higher elevations.

Other at-risk species (the little brown bat (*Myotis lucifugus*), and tri-colored bat (*Perimyotis subflavus*)) had modest occupancy estimates (both  $\psi = 0.46$ ) and were found in more forested areas and at higher elevations. The eastern small-footed bat (*Myotis leibii*), a North Carolina species of concern, had a higher occupancy estimate ( $\psi = 0.61$ ) and occurred more commonly at higher elevations. Historically abundant species including the big brown bat, (*Eptesicus fuscus*), the hoary bat (*Lasiurus cinereus*), and the eastern red bat, (*Lasiurus borealis*), had relatively high occupancy estimates ( $\psi$  range: 0.62 - 0.73) and temperature and distance to water predicted their occupancy. Occupancy of the evening bat (*Nycticeius humeralis*), and silver haired bat (*Lasionycteris noctivagans*) was modest ( $\psi = 0.44$ ,  $\psi = 0.49$ , respectively), and was best predicted by percent forest, distance to water, and elevation. As bats influence ecosystem health and insect abundance, supporting these species as efficiently as possible is essential, not only for bat conservation, but for the preservation of ecosystem balance.

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## TABLE OF CONTENTS

Abstract.....	iv
Acknowledgments .....	vi
List of Tables .....	viii
List of Figures.....	ix
Keywords & Introduction .....	1
Study Area.....	4
Methods.....	5
Results.....	10
Discussion.....	33
Management Implications.....	38
References.....	40
Vita.....	56

## LIST OF TABLES

Table 1. Bat species historically detected on the Blue Ridge Parkway .....	17
Table 2. 2021 survey sites and number of survey nights .....	19
Table 3. Covariates used in occupancy modeling .....	22
Table 4. Competing site-occupancy models .....	23
Table 5. Model-averaged occupancy estimates .....	27



## LIST OF FIGURES

Figure 1. Map of all survey sites.....	29
Figure 2. Location of listed species on the parkway, sites 1-12 .....	29
Figure 3. Location of listed species on the parkway, sites 13-28 .....	30
Figure 4. Location of listed species on the parkway, sites 29-40 .....	30
Figure 5. Location of listed species on the parkway, sites 41-49 .....	31
Figure 6. Location of listed species on the parkway, sites 50-59 .....	31
Figure 7. Modeled patterns between occupancy and temperature .....	32

**KEYWORDS** Bat occupancy, Blue Ridge Parkway *Corynorhinus townsendii virginianus*, *Eptesicus fuscus*, foraging habitat, *Lasionycteris noctivagans*, *Lasiurus borealis*, *Lasiurus cinereus*, *Myotis grisescens*, *Myotis leibii*, *Myotis lucifugus*, *Myotis septentrionalis*, *Myotis sodalis*, North Carolina, *Nycticeius humeralis*, *Perimyotis subflavus*.

## INTRODUCTION

Bat populations in North America are facing pressure from disease and anthropogenic change, including climate change and land cover alterations. Severe declines in bat abundance and diversity may negatively impact the functional diversity of communities and ecosystems (Gorresen et al. 2008). Insectivorous bats have important ecological roles including insect suppression, and material and nutrient distribution, consuming more than 25% of their body mass in insects each night (Coutts et al. 1973). For example, the little brown bat (*Myotis lucifugus*) consumes over 100% of its body mass in insects during the peak night of its lactation (Kurta et al. 1989). Thus, bats control insect populations which can directly influence plant communities and indirectly influence herbivore communities; as nocturnal predators of crop pests, it is estimated that bats provide services to agriculture equaling several billions of dollars each year (Schmitz and Suttle 2001, Boyles et al. 2011, Kasso and Balakrishnan 2013).

Populations of many true-hibernating, cave-dwelling species of bats are plummeting due to the introduced psychrophilic fungus (*Pseudogymnoascus destructans*) which is responsible for the white-nose syndrome (WNS) epidemic. First detected in New York in 2006, *Pseudogymnoascus destructans* spread quickly to almost every U.S state and Canadian province, killing millions of bats (Verant et al. 2014). Mortality rates in WNS-affected colonies often

exceed 90 percent, and regional extinction of previously abundant species has been predicted (Wilder et al. 2011). Several species that were once common, particularly species of the genus *Myotis*, are now at risk of extinction (Lorch et al. 2016). The little brown bat's rapid decline due to white-nose syndrome prompted research that predicted a 99% likelihood of species extinction by 2030 (Frick et al. 2010). In New Hampshire, multi-summer capture rates show three *Myotis* species have declined by 68–98 percent (Moosman et al. 2013). Similarly, in West Virginia, four *Myotis* species have declined by 77–90 percent (Francl et al. 2012). In the southern Appalachian forests of North Carolina and Tennessee, four once-common species (the little brown bat, Indiana bat (*Myotis sodalis*), northern long-eared bat (*Myotis septentrionalis*), and tri-colored bat (*Perimyotis subflavus*)) declined by 82–99 percent from 2009 to 2016 (O'Keefe et al. 2019).

Effective conservation strategies for bat populations require population monitoring and analyses. Compared to conventional capture methods, automated detection of echolocation calls provides an efficient means of sampling bat activity, particularly when done simultaneously at multiple sites and over long time periods (Murray et al. 1999, Miller 2001). Occupancy analysis and its ability to account for differential detection ( $p$ ) probabilities, is a valuable technique when echolocation call detection is used as a measure of bat occurrence and activity (Gorresen et al. 2008). Developments in techniques for modeling animal occupancy ( $\psi$ ) and detection probability ( $p$ ), coupled with echolocation detection, present an opportunity for the study of bat distribution and habitat use.

Because landscape structure affects bat foraging activity and occupancy (Gehrt and Chelsvig 2003), an understanding of how land use characteristics predict occupancy can enable managers to better delineate critical habitat for rare species. For example, larger bat species are

more likely to be detected in open habitats (Brooks et al. 2017) while smaller bat species, including members of the WNS susceptible *Myotis* genus, are often recorded in forested habitats (Starbuck et al. 2015). Other factors that may affect selection of foraging patches include distance to water (e.g., Krusic et al. 1996, Humes et al. 1999, Erickson and West 2003, Brooks 2009) and elevation (e.g., Grindal and Bringham, 1999). While some research (e.g., Ford et al. 2005) reports increased bat detection near bodies of water, a study in the southern Appalachian mountains found bats were more likely to be detected at lower elevations with no influence of distance to water (Brooks et al. 2017). Further, abiotic factors like precipitation and temperature may affect the likelihood of documenting bat foraging calls (Appel et al. 2019). Temperature and rain can affect insect prey abundance, influence thermoregulation and flight ability and thus affect bat foraging behavior (Rydell et al. 1996, Agosta et al. 2005, Reynolds 2006).

On the North Carolina portion of the Blue Ridge Parkway (BRP), 14 species of bats have been detected historically (Graeter et al. 2015, Table 1). Of these, 50% are susceptible to WNS disease and four species are federally listed: Virginia big-eared, gray, northern long-eared, and Indiana bat. The Virginia big-eared bat, though not susceptible to WNS, is a rare species experiencing declines unrelated to the epidemic. Here, I examine species occupancy ( $\psi$ ) for bats on the North Carolina portion of the Blue Ridge Parkway. Overall, I predicted occupancy would be lower for species reporting declines pre and post-WNS (Virginia big-eared bat (*Corynorhinus townsendii virginianus*), gray bat (*Myotis grisescens*), Indiana bat, northern long-eared bat, tri-colored bat, little brown bat, and eastern small-footed bat (*Myotis leibii*)) compared to species that are either not susceptible to the disease or have not reported extreme declines due to the disease (silver-haired bat (*Lasionycteris noctivagans*), evening bat (*Nycticeius humeralis*),

eastern red bat (*Lasiurus borealis*), hoary bat (*Lasiurus cinereus*) and big brown bat (*Eptesicus fuscus*). Further, I investigated how habitat characteristics affected occupancy. I expected forest cover to be related to body size such that larger bat species might be more common in less forested habitats. I also predicted bat species with higher echolocation call frequencies to occupy forested habitats (*Myotis spp.*). Finally, I expected that elevation might influence occupancy of hoary bat and silver-haired bat (Diggins and Ford 2022), and that bats might be more likely to occupy sites with warmer temperatures.

## STUDY AREA

During the summer of 2021, I conducted 59 stationary acoustic bat surveys along the Blue Ridge Parkway in montane Western North Carolina, starting at the Virginia / North Carolina state line (milepost 217, Cumberland Knob), extending down to the southern terminus of the Parkway (milepost 469, Figure 1, Table 2). Each site was surveyed from 4-8 nights. Survey points spanned an elevation gradient of 669.9 - 1776.9 m, the percent forest coverage varied from 47.8 - 96.3% and sites varied from 12.5 - 547.9 m from water (Table 3). I established survey points from June 17 - July 28, 2021, within the U.S. Fish and Wildlife Service and North American Bat Monitoring Program (NABat) protocol window guidelines (Loeb et al. 2015, U.S.F.W.S. 2020, 2021). Previous studies have noted difficulty in detecting some species during winter hibernacula surveys, including the northern long-eared bat and eastern small-footed bat (Moosman et al. 2013). The summer season (specifically June - July) was the selected timeframe for this study's data collection, as population dynamics may be more accurately recorded; maternal colonies are active in early summer, feeding their young, and pups begin to hunt for themselves in late summer (O'Keefe et al. 2019).

## METHODS

### Detector Deployment

Detectors monitored 33 developed areas (campgrounds, picnic areas, visitor attractions, maintenance areas, etc.) requested by the National Park Service as these areas are subject to park development, recreation, tree removal, etc. I recorded data for a minimum of 8 nights, in accordance with the Endangered Species Act, NABat protocol, and U.S. Fish and Wildlife Service acoustic monitoring guidelines for listed species (Federal Register 2013, Loeb et al. 2015, Table 2). Also, I conducted 26 supplementary surveys in areas with less development and less human impact. These sites were carefully chosen for their biological relevance, with the aim of seeking greater diversity of species and landscapes to gain insight into foraging habitat preferences. I monitored these supplementary survey sites for a minimum of four nights in accordance with NABat stationary point acoustic survey guidelines and additional sampling duration research (Skalak et al. 2012, Loeb et al. 2015, U.S.F.W.S. 2020, 2021, Table 2).

I strategically placed Anabat Express zero-crossing, frequency-division bat detectors no further than 14 kilometers apart to account for known bat foraging distances (Henry et al. 2002, Murray and Kurta 2004). I mounted omnidirectional ultrasonic microphones in parabolic adapters approximately 2.5 m above the ground at sites using steel poles and rebars (Titley Electronics, Columbia, Missouri, USA). Microphone orientation varied, and was chosen in favor of open space, 3-5 meters from clutter, in accordance with NABat protocol (Loeb et al. 2015). Anabat Express detectors recorded bat echolocation passes from 1 hour prior to sunset until 1 hour after sunrise each night. All sounds registered by the microphone were stored for analysis. Universal Transverse Mercator coordinates, weather conditions, and Parkway milepost were also

recorded. I used ArcMap v10.8.1 to construct maps of the completed survey locations and bat species detections (ESRI 2020).

### **Bat Call Identification**

As bat species produce unique echolocation calls, software programs and manual vetting can be utilized to analyze the acoustic characteristics of recorded calls, and identify the species responsible for each call recorded to estimate species detection. The accuracy of these algorithms is dependent on the quality of the “training data set” used during the initial set-up (Fraser et al. 2020). Though confidence in call identification can be strengthened through the application of multiple analysis strategies, researchers recognize that several bat species are difficult to identify from their calls, making definitive acoustic classification impossible in some cases.

Using echolocation calls to identify bats species can be challenging due to a variety of factors including technology limitations, methodology, and the ability to capture high-quality, representative calls. The most influential factor is overlap in call characteristics between many species (Fraser et al. 2020). While automatic identification tools are convenient and can recognize species with unique calls reliably, this method is often inaccurate when attempting to distinguish between species with overlapping call characteristics (Rydell et al. 2017). Szewczak et al. (2011) reported automatic ID software frequently misidentifying the call of the little brown bat as that of the Indiana bat as the two species’ calls have significant overlap in duration, characteristic frequency, start slope, and other call characteristics. Even call identifications at the genus level can be very useful precursors to future identification via mist-netting. In some cases,

manual call identification has shown a higher classification success compared to automated software (Rydell et al. 2017).

Acoustic data files recorded at survey sites were screened for species of bats historically detected on the Blue Ridge Parkway in North Carolina (Table 1). Acoustic identification of bat species' echolocation pulses was performed using Kaleidoscope Pro v5.4.0 and BCID v2.8b (Wildlife Acoustics 2018, BCID 2019), both of which were approved by the U.S Fish and Wildlife Service (U.S.F.W.S.) for 2021 Indiana and northern long-eared bat survey protocol. I determined bat species detection at a site only if identified calls had a maximum likelihood estimator (MLE) of misclassification at the species level of  $\alpha = 0.05$  or less, and if species identification at the point was agreed upon by both Kaleidoscope Pro and BCID.

To ensure a higher level of confidence in identification, in addition to automatic software identification, calls were manually identified using the program Anabat Insight (Russo and Voigt 2016). This involved analyzing spectrogram call images, and in some cases, zero-crossing imaging (distinction of *Myotis* species). Manually assessed call recordings were only included if the sound quality was sufficient to clearly see identifying features and distinguish from similar species with confidence. Only search phase calls were analyzed. Call characteristics considered included lowest frequency, highest frequency, characteristic frequency, duration, bandwidth, and call shape. Kilohertz (kHz) was the unit used to measure frequency (cycles per second). These characteristics have been described as standard parameters for identification (Fenton and Bell 1979, O'Farrell et al. 1999, Goudy-Trainor and Freeman 2002). The frequency with maximum



energy (fmaxE) occurs in the outward pulse of a call. This was also included, as it was described by Fullard et al. (1991) as one of the most consistent and critical echolocation call parameters.

Any individual bat may emit calls beyond typical ranges and beyond the call characteristics listed in this dataset. These measurements are unlikely to be definitive descriptions of these species' acoustic characteristics. A probability ( $P$ ) value was generated for each automatic call identification. Bat group or species presence was only confirmed if both software agreed on the species identified with  $P$ -values  $\leq 0.05$ , and if further identification was confirmed via confident manual identification. All calls for rare threatened and endangered species were manually vetted and hand verified by M. St. Germain.

### **Defining Landscape Characteristics**

To identify correlations between species occupancy and habitat characteristics, I applied physiographic variables and forest structure variables when modeling occupancy (Blakey et al. 2019). Site-level covariates included: elevation (m), percent of land cover, and nearest distance to water (m). As the Parkway (road) was consistently present throughout the field site, relative to bat foraging distances, proximity to the nearest road was not included as a covariate. Using ArcGIS, I recorded the elevation at each detector's longitudinal and latitudinal coordinates. I used the U.S. Geological Survey National Hydrography Dataset Best Resolution (NHD)- North Carolina (updated: 2022-01-31) to determine the nearest distance to water (m) from each detector.

To determine the percent of land cover that was forested, I used the 2016 forest land cover data from the N.C. Department of Agriculture & Consumer Services (N.C.D.A. & C.S.).

Forest land cover data was derived from the North Carolina, 4 band, 2016, U.S.D.A. National Agriculture Imagery Program (N.A.I.P.). These data were chosen for its 1 m pixel resolution and its estimated ~5% error or misclassification rate. Land cover was classified as Forest/Trees, or Non-forest/trees. Texture processing was applied to reduce mixed pixel values between tree canopy, healthy grass and agriculture land areas, as these land cover types have similar vegetation spectral response. I quantified the percent forested land cover within a 1 km radius of each detector. I chose a 1 km radius to account for known species foraging distances and to reduce the risk of site overlap (Henry et al. 2002, Murray and Kurta 2004, Luo et al. 2019).

### **Occupancy Modeling and Analysis**

I used site-occupancy models to identify relationships between bat species presence and foraging habitat characteristics, while accounting for imperfect detection of species (Yates and Muzika 2006, Gorresen et al. 2008, Hein et al. 2009, MacKenzie et al. 2017). I conducted single-season occupancy analyses (Royle and Nichols 2003, MacKenzie et al. 2017) with the program PRESENCE (version 2.13.47) for each of the 12 species.

The following site-level habitat characteristics were included when modeling: elevation, percent forest land cover within a 1 km radius, and nearest distance to water. As weather is likely to influence nightly bat activity, I included the following sampling (detection) covariates: maximum temperature (°C), minimum temperature (°C), and 24-hour precipitation (cm) (Rydell et al. 1996, Agosta et al. 2005, Reynolds 2006, Voigt et al. 2011). Maximum temperature, minimum temperature, and precipitation data for each point were gleaned from N.O.A.A. stations closest to each site (Table 3). All covariates were standardized (z-score) before being entered into PRESENCE.

I ran time models for each species to account for variation in occupancy over the course of the season due to the activities of lactating maternal colonies, detection of newly-volant pups, and migration (Johnson et al. 2008, Turbill 2008, Blakey et al. 2019).

I first determined the best model for estimating  $p$  and then included the covariates from the best model for  $p$  while evaluating covariates for  $\psi$ . I then evaluated the relationship of  $\psi$  with all six sample and site-level covariates. “Absences” may more accurately reflect “no detection.” Mean detection probabilities were calculated to assess the likelihood of detection. Next, I ran goodness of fit tests to assess tolerance of all models; models only met goodness of fit standards if  $\hat{c} < 4$ . All models met this standard with the exception of two species. I identified competing models by comparing Akaike’s Information Criteria (AIC); models with  $\Delta\text{AIC} < 2$  were considered competing. I compared model-averaged  $\psi$  for all species. I present the effects of some covariates by plotting predictions of  $\psi$  for each detection site (Figure 7).

## RESULTS

I obtained interpretable acoustic data from all 59 survey sites along BRP in North Carolina. The dataset initially consisted of 412 survey nights, with detectors failing 9 nights, resulting in 403 survey nights.

Twelve bat species were detected, including four federally endangered species: the Virginia big-eared bat, the gray bat, the northern long-eared bat, and the Indiana bat. I also detected one proposed federally endangered species: the tri-colored bat and one North Carolina species of special concern: the eastern small-footed bat. Additionally, I detected one bat species

with an “at risk” listing status currently under federal review (due to declining population sizes): the little brown bat (Tables 1 and 4). Federally-listed bat species were detected at 33 of the 59 sites. I detected other species including the big brown bat, the eastern red bat, the hoary bat, the silver-haired bat, and the evening bat (Figures 2-6).

At several sites a high number of calls were reported; 2,862 calls were detected at Linville Falls: Campground (8 nights) and 2,643 calls were detected at Bengie Maintenance Area (8 nights). The greatest species richness, 10 species, was recorded at site FH 18: Rich Mountain. Twelve sites had eight or more species detected. Survey sites with the lowest diversity included: FH 1: Parkway right, FH 9: Parkway left, FH 11: Parkway right, FH 16: Boone Fork trailhead, and FH 24: MTS Trailhead, Parkway right.

### **Virginia big-eared bat**

I detected Virginia big-eared bats at 21 of the 59 sites and 10.9% of nights. The top ranking occupancy model ( $\psi$  (constant),  $p$  (maximum temperature, elevation)) showed a positive relationship between detectability and maximum temperature ( $beta = 8.08$ ) and a negative relationship between elevation and detection ( $beta = -0.40$ , Table 4) and average  $p$  (detection) = 0.24. The top model for estimating occupancy was the null model, suggesting there was no relationship between occupancy and site or sampling characteristics. Seven other competing models included the covariates of nearest distance to water, minimum temperature, precipitation, elevation, and percent of forested land cover within the 1 km radius (Table 4). Occupancy of Virginia big-eared bat was  $\psi$  ( $SE$ ) =  $0.45 \pm 0.08$  (Table 5) and there was no evidence to suggest lack of fit for the global model ( $\hat{c} = 1.66$ ).

### Big brown bat

I detected big brown bats at 43 of the 59 sites and 61.53% of nights. The top ranking occupancy model ( $\psi$  (minimum temperature),  $p$  (maximum temperature, nearest distance to water)) showed a positive relationship between detection and maximum temperature and distance to water ( $beta = 1.39$  and  $0.35$ ) and a negative relationship between minimum temperature occupancy ( $beta = -0.88$ , Table 4) and average  $p = 0.77$ . Big brown bats were more likely to occupy locations sampled during lower minimum temperatures (Figure 7a). Occupancy of the big brown bat was  $\psi (SE) = 0.73 \pm 0.07$  (Table 5), however, all models lacked goodness of fit, signifying possible overdispersion of the data ( $\hat{c} = 19.12$ ). There was one other competing model that also included the covariates of minimum temperature, maximum temperature, and nearest distance to water (Table 4).

### Eastern red bat

I detected eastern red bats at 36 of the 59 sites and 38.21% of nights. The top ranking occupancy model ( $\psi$  (distance to water, minimum temperature),  $p$  (% forested)) showed a negative relationship between detection and % forested land cover ( $beta = -2.30$ ), a negative relationship between occupancy and minimum temperature ( $beta = -0.65$ ), and a positive relationship between occupancy and distance to water ( $beta = 0.95$ , Table 4) and average  $p = 0.55$ . Eastern red bats were more likely to occupy locations farther from water and those sampled during lower minimum temperatures (Figure 7b). There were no other competing models for occupancy of this species (Table 4). Occupancy of the eastern red bat was  $\psi (SE) = 0.62 \pm 0.09$  (Table 5) and the model met goodness of fit standards ( $\hat{c} = 0.99$ ).

### Hoary bat

I detected hoary bats at 37 of the 59 sites and 38.21% of nights. The top ranking occupancy model ( $\psi$  (distance to water, maximum temperature),  $p$  (constant)) showed no relationship between detection and the habitat and sampling variables. There was a negative relationship between occupancy and maximum temperature ( $beta = -0.62$ ), and a positive relationship between occupancy and distance to water ( $beta = 0.46$ , Table 4) and average  $p = 0.64$ . Hoary bats were more likely to occupy locations farther from water and with lower maximum temperatures (Figure 7d). Occupancy of the hoary bat was  $\psi (SE) = 0.63 \pm 0.10$  (Table 5) and the model met goodness of fit standards ( $\hat{c} = 3.42$ ).

### Silver-haired bat

I detected silver-haired bats at 25 of the 59 sites and 18.61% of nights. The top ranking occupancy model ( $\psi$  (distance to water),  $p$  (elevation)) showed a negative relationship between detection and elevation ( $beta = -0.60$ ) and a positive relationship between occupancy and distance to water ( $beta = 0.41$ , Table 4) and average  $p = 0.35$ . Silver-haired bats were more likely to occupy locations farther from water. Occupancy of the silver-haired bat was  $\psi (SE) = 0.49 \pm 0.10$  (Table 5) and the model met goodness of fit standards ( $\hat{c} = 0.87$ ).

### Gray bat

I detected gray bats at 8 of the 59 sites and 2.72% of nights. The top ranking occupancy model ( $\psi$  (constant),  $p$  (maximum temperature)) showed a positive relationship between detection and the maximum temperature ( $beta = 0.62$ ). There was no relationship or pattern between

occupancy and the habitat and sampling variables (Table 4) and average  $p = 0.12$ . Occupancy of the gray bat was  $\psi (SE) = 0.23 \pm 0.10$  (Table 5) and the model met goodness of fit standards ( $\hat{c} = 3.36$ ).

### **Eastern small-footed bat**

I detected eastern small-footed bats at 31 of the 59 sites and 20.59% of nights. The top ranking occupancy model ( $\psi$  (constant),  $p$  (elevation)) showed a positive relationship between detection and elevation ( $beta = 0.63$ ) and no relationship between occupancy habitat and sampling variables (Table 4) and average  $p = 0.32$ . The top model for estimating occupancy was the null model. Occupancy of the eastern small-footed bat was  $\psi (SE) = 0.61 \pm 0.078$  (Table 5) and the model met goodness of fit standards ( $\hat{c} = 0.99$ ).

### **Little brown bat**

I detected little brown bats at 12 of the 59 sites and 5.21% of nights. The top ranking occupancy model ( $\psi$  (%forested),  $p$  (% forested)) showed a strong positive relationship between detection and percent forested land cover ( $beta = 9.31$ ), and a strong negative relationship between occupancy and percent forested land cover ( $beta = -16.12$ , Table 4) and average  $p = 0.19$ . Little brown bats were more likely to occupy locations with less forest cover. Occupancy of the little brown bat was  $\psi (SE) = 0.47 \pm 0.10$  (Table 5) and the model met goodness of fit standards ( $\hat{c} = 0.84$ ).

### **Northern long-eared bat**

I detected northern long-eared bats at 18 of the 59 sites and 12.9% of nights. The top ranking occupancy model ( $\psi$  (elevation),  $p$  (elevation, precipitation)) showed a positive relationship between detection and elevation ( $beta = 0.38$ ), a negative relationship between detection and precipitation ( $beta = -0.86$ , Table 4) and average  $p = 0.35$ . The model also showed a positive relationship between occupancy and elevation ( $beta = 0.90$ ). Northern long-eared bats were more likely to occupy locations at higher elevations. There were no other competing models for occupancy of this species (Table 4). Occupancy of the northern long-eared bat was  $\psi (SE) = 0.33 \pm 0.08$  (Table 5) and the model met goodness of fit standards ( $\hat{c} = 0.78$ ).

### **Indiana bat**

I detected Indiana bats at 18 of the 59 sites and 10.91% of nights. The top ranking occupancy model ( $\psi$  (maximum temperature, elevation),  $p$  (distance to water)) showed a positive relationship between detection and distance to water ( $beta = 0.39$ ), a negative relationship between occupancy and maximum temperature ( $beta = -0.79$ ), and a positive relationship between occupancy and elevation ( $beta = 0.70$ , Table 4) and average  $p = 0.29$ . Indiana bats were more likely to occupy locations sampled at lower maximum temperatures (Figure 7c) and at higher elevations. There was one other competing model that included percent forested land cover in addition to maximum temperature, elevation, and nearest distance to water (Table 4). Occupancy of the Indiana bat was  $\psi (SE) = 0.37 \pm 0.11$  (Table 5) and the model met goodness of fit standards ( $\hat{c} = 0.96$ ).



### Evening Bat

I detected evening bats at 22 of the 59 sites and 15.63% of nights. The top ranking occupancy model ( $\psi$  (minimum temperature),  $p$  (% forested)) showed a strong positive relationship between detection and percent forested land cover ( $beta = 6.42$ ), and average  $p = 0.33$ . There was a negative relationship between occupancy and minimum temperature ( $beta = -0.49$ , Table 4). Evening bats were more likely to occupy locations sampled at lower minimum temperatures (Figure 7e). There were five other competing models that included minimum temperature, maximum temperature, elevation, percent forested land cover within a 1 km radius, and nearest distance to water (Table 4). Occupancy of the evening bat was  $\psi (SE) = 0.44 \pm SE 0.10$  (Table 5) and the model met goodness of fit standards ( $\hat{c} = 0.74$ ).

### Tri-colored Bat

I detected tri-colored bats at 22 of the 59 sites and 10.42% of nights. The top ranking occupancy model ( $\psi$  (maximum temperature, elevation),  $p$  (constant)) showed no pattern between detection and site and sampling characteristics, and average  $p = 0.24$  (Table 4). There was a positive relationship between occupancy and maximum temperature ( $beta = 0.54$ ), and a positive relationship between occupancy and elevation ( $beta = 0.84$ ). Tri-colored bats were more likely to occupy locations sampled at higher maximum temperatures (Figure 7f) and at higher elevations. Occupancy of the tri-colored bat was  $\psi (SE) = 0.46 \pm 0.12$  (Table 5), however, these models did not meet goodness of fit standards ( $\hat{c} = 5.95$ ). There were two other competing models that described patterns between occupancy elevation, maximum temperature, and percent forested land cover (Table 4).

Table 1. Bat species historically detected on the Blue Ridge Parkway in North Carolina, conservation listings, White Nose Syndrome (WNS) susceptibility, and whether the species was detected in the 2021 surveys.

Common name	Species	Species code	Conservation status	WNS susceptibility	2021 detection
Rafinesque's big-eared bat	<i>Corynorhinus rafinesquii</i>	CORA	**NC Threatened	<sup>a</sup> <i>P. destructans</i> positive	
Virginia big-eared bat	<i>Corynorhinus townsendii virginianus</i>	COTO	**Federally Endangered	<i>P. destructans</i> positive	Yes
Big brown bat	<i>Eptesicus fuscus</i>	EPFU	Common	<sup>b</sup> Confirmed symptomatic	Yes
Silver-haired bat	<i>Lasionycteris noctivagans</i>	LANO	Uncommon	<i>P. destructans</i> positive	Yes
Eastern red bat	<i>Lasiurus borealis</i>	LABO	Common	<i>P. destructans</i> positive	Yes
Hoary bat	<i>Lasiurus cinereus</i>	LACI	Common		Yes
Gray bat	<i>Myotis grisescens</i>	MYGR	**Federally Endangered	Confirmed symptomatic	Yes

Common name	Species	Species code	Conservation status	WNS susceptibility	2021 detection
Eastern small-footed bat	<i>Myotis leibii</i>	MYLE	*NC Species of Concern	Confirmed symptomatic	Yes
Little brown bat	<i>Myotis lucifugus</i>	MYLU	**"At Risk" under federal review	Confirmed symptomatic	Yes
Northern long-eared bat	<i>Myotis septentrionalis</i>	MYSE	**Federally Endangered	Confirmed symptomatic	Yes
Indiana bat	<i>Myotis sodalis</i>	MYSO	**Federally Endangered	Confirmed symptomatic	Yes
Evening bat	<i>Nycticeius humeralis</i>	NYHU	Common		Yes
Tri-colored bat	<i>Perimyotis subflavus</i>	PESU	**Proposed Fed. Endangered	Confirmed symptomatic	Yes
Mexican free-tailed bat	<i>Tadarida brasiliensis</i>	TABR	Common	<i>P. destructans</i> positive	

<sup>a</sup>*P. destructans* positive: indicates that the species has tested positive for the fungus, but does not appear to be symptomatic or experience population declines due to WNS (Muller et al. 2013).

<sup>b</sup>Confirmed symptomatic: species that have experienced symptoms and population declines due to WNS (Frick et al. 2015).

Table 2. 2021 survey sites and number of survey nights per site for bat occupancy on the Blue Ridge Parkway in North Carolina

<b>Survey Site</b>	<b>No. of survey nights</b>
Cumberland Knob Gully Creek Trailhead	8
FH <sup>a</sup> 26: Pond, Parkway left	8
FH 25: Creek, field and woods	8
Doughton Park: Brinegar Cabin	8
Doughton Park: Campground	8
FH 24: MTS Trailhead, Parkway right	8
Doughton Park: Bluffs Lodge	8
FH 23: Bluff Mtn Trail field	8
Bluffs Maintenance Area	8
FH 22: Pasture, Parkway right	8
Northwest Trading Post	8
FH 21: Parkway right, powerline left of drainage	8
Benge Maintenance Area	8
Jeffress Park: The Cascades	8
Jeffress Park: Cool Springs Baptist Church	8
FH 20: Parkway left, field	8
FH 19: Goshen Creek Branch Trail	8
Moses H. Cone Memorial Park: Manor	8
Moses H. Cone Memorial Park: Sandy Flat Office	8
Moses H. Cone Memorial Park: Bass Lake	8
FH 18: Rich Mountain	8
FH 17: Firetower Trail	8

<b>Survey Site</b>	<b>No. of survey nights</b>
Julian Price Park Memorial Park: Sims Pond	8
Julian Price Park Memorial Park: Pasture	8
Julian Price Park Memorial Park: Campground	8
FH 16: Boone Fork Trailhead	4
Linn Cove Visitor Center	8
FH 15: View Lost Cove Cliffs	4
Linville Falls: Picnic Area	8
Linville Falls: Campground	8
FH 14: Pasture, Parkway right	4
Gillespie Gap Ranger Housing	8
FH 13: Parkway right	4
Crabtree Falls: Campground	8
Crabtree Falls: Picnic Area	8
FH 12: Parkway right	4
FH 11: Parkway right	4
Craggy Gardens Visitor Center	8
Craggy Gardens Picnic Area	8
FH 10: Parkway left	3
FH 9: Parkway left	4
Oteen: Folk Art Center	8
Oteen: Maintenance Area & Ranger Housing	6
Headquarters	8
FH 8	4
FH 7: South of Beaver Dan Gap Overlook	4
Pisgah Picnic Area	7

<b>Survey Site</b>	<b>No. of survey nights</b>
Pisgah Campground	8
Wagon Road Maintenance Area	7
FH 6	5
Graveyard Fields Restroom Facility	8
FH 5: Parkway left	4
FH 4: Overlook North of Balsam, parkway right	4
Balsam Gap Maintenance Area & Ranger HQ	8
FH 3: Parkway left	3
Waterrock Knob	8
Soco Gap	8
FH 2: Parkway right	4
FH 1: Parkway right	4

<sup>a</sup>FH= sites selected for the purpose of surveying foraging habitats. All other sites requested by the National Park Service.

Table 3. Minimum, maximum, mean, and standard error of covariates that were used in occupancy modeling of bats on the Blue Ridge Parkway in North Carolina, USA, during the summer of 2021.

Covariate	<i>Min.</i>	<i>Max.</i>	<i>Mean</i>	<i>SE</i>
Elevation (m)	669.9	1776.9	1141.3	34.6
% forest (1 km radius)	47.8	96.2	79.5	1.6
Distance to water (m)	12.5	547.9	206.8	17.4
Maximum temperature (°C)	17.2	32.7	26	0.1
Minimum temperature (°C)	6.1	21.1	14.4	0.1
Precipitation (cm)	0	6.3	0.5	0.057

Table 4. The competing site-occupancy models ( $\Delta AIC < 2$ ) for the twelve bat species detected on the Blue Ridge Parkway, NC, USA, in 2021 including the Akaike's Information Criterion (AIC), delta AIC ( $\Delta AIC$ ), and AIC weight, the log likelihood (LogLik), and the number of model parameters (No. Par.) for each model. Each listed model involves covariates accounting for the probability a species occupied a site ( $\Psi$ ), and considers the the probability of species detection, given it is present at a site ( $p$ ).

Models <sup>a</sup> by species	<i>AIC</i>	$\Delta AIC$	<i>AIC Weight</i>	<i>LogLik</i>	<i>No. Par.</i>
Virginia big-eared bat					
$\Psi$ (.) <sup>b</sup> , $p$ (max temp, elevation)	249.73	0	0.173	1	4
$\Psi$ (water), $p$ (max temp, elevation)	251.17	1.44	0.0842	0.4868	5
$\Psi$ (min temp), $p$ (max temp, elevation)	251.42	1.69	0.0743	0.4296	5
$\Psi$ (.), $p$ (max temp)	251.45	1.72	0.0732	0.4232	3
$\Psi$ (precipitation), $p$ (max temp, elevation)	251.63	1.9	0.0669	0.3867	5
$\Psi$ (elevation), $p$ (max temp, elevation)	251.67	1.94	0.0656	0.3791	5
$\Psi$ (max temp), $p$ (max temp, elevation)	251.68	1.95	0.0653	0.3772	5
Big brown bat					
$\psi$ (min temp), $p$ (max temp, water)	399.14	0	0.4592	1	5
$\psi$ (min temp, water), $p$ (max temp, water)	399.5	0.36	0.3836	0.8353	6



Models <sup>a</sup> by species	<i>AIC</i>	$\Delta AIC$	<i>AIC Weight</i>	<i>LogLik</i>	<i>No. Par.</i>
Eastern red bat					
$\Psi$ (water, min temp), <i>p</i> (%forest)	435.56	0	0.7852	1	5
Hoary bat					
$\Psi$ (max temp, water), <i>p</i> (.)	426.04	0	0.2288	1	4
$\Psi$ (max temp), <i>p</i> (.)	426.52	0.48	0.1799	0.7866	3
$\Psi$ (max temp, water, %forest), <i>p</i> (.)	427.79	1.75	0.0954	0.4169	5
Silver-haired bat					
$\Psi$ (water), <i>p</i> (elevation)	327.88	0	0.1703	1	4
$\Psi$ (.), <i>p</i> (elevation)	327.93	0.05	0.1661	0.9753	3
$\Psi$ (precipitation), <i>p</i> (elevation)	328.65	0.77	0.1159	0.6805	4
$\Psi$ (water, precipitation), <i>p</i> (elevation)	329.03	1.15	0.0958	0.5627	5
$\Psi$ (min temp), <i>p</i> (elevation)	329.68	1.8	0.0692	0.4066	4
$\Psi$ (water, elevation), <i>p</i> (elevation)	329.73	1.85	0.0675	0.3965	5
$\Psi$ (water, min temp), <i>p</i> (elevation)	329.82	1.94	0.0646	0.3791	5
$\Psi$ (elevation), <i>p</i> (elevation)	329.86	1.98	0.0633	0.3716	4
Gray bat					
$\Psi$ (.), <i>p</i> (max temp)	98.18	0	0.156	1	3
$\Psi$ (water), <i>p</i> (max temp)	98.68	0.5	0.1215	0.7788	4
$\Psi$ (%forest), <i>p</i> (max temp)	99.31	1.13	0.0887	0.5684	4
$\Psi$ (.), <i>p</i> (.)	99.31	1.13	0.0887	0.5684	2
$\Psi$ (.), <i>p</i> (precipitation)	99.55	1.37	0.0786	0.5041	3
$\Psi$ (water, %forest), <i>p</i> (max temp)	99.62	1.44	0.0759	0.4868	5

Models <sup>a</sup> by species	<i>AIC</i>	$\Delta AIC$	<i>AIC Weight</i>	<i>LogLik</i>	<i>No. Par.</i>
$\Psi$ (elevation), <i>p</i> (max temp)	99.99	1.81	0.0631	0.4045	4
$\Psi$ (precipitation), <i>p</i> (max temp)	100.16	1.98	0.058	0.3716	4
$\Psi$ (max temp), <i>p</i> (max temp)	100.17	1.99	0.0577	0.3697	4
$\Psi$ (min temp), <i>p</i> (max temp)	100.17	1.99	0.0577	0.3697	4
Eastern small-footed bat					
$\Psi$ (.), <i>p</i> (elevation)	360.6	0	0.2499	1	3
$\Psi$ (water), <i>p</i> (elevation)	362.01	1.41	0.1235	0.4941	4
$\Psi$ (precipitation), <i>p</i> (elevation)	362.03	1.43	0.1223	0.4892	4
$\Psi$ (.), <i>p</i> (elevation, %forest)	362.18	1.58	0.1134	0.4538	4
$\Psi$ (elevation), <i>p</i> (elevation)	362.46	1.86	0.0986	0.3946	4
$\Psi$ (min temp), <i>p</i> (elevation)	362.47	1.87	0.0981	0.3926	4
$\Psi$ (1kmforest), <i>p</i> (elevation)	362.5	1.9	0.0967	0.3867	4
$\Psi$ (max temp), <i>p</i> (elevation)	362.55	1.95	0.0943	0.3772	4
Little brown bat					
$\Psi$ (%forest), <i>p</i> (%forest)	152.33	0	0.1984	1	4
$\Psi$ (.), <i>p</i> (%forest)	153.72	1.39	0.099	0.4991	3
$\Psi$ (.), <i>p</i> (.)	153.88	1.55	0.0914	0.4607	2
$\Psi$ (%forest, water), <i>p</i> (%forest)	153.97	1.64	0.0874	0.4404	5
$\Psi$ (.), <i>p</i> (elevation)	154.21	1.88	0.0775	0.3906	3
Northern long-eared bat					
$\Psi$ (elevation), <i>p</i> (elevation, precipitation)	237.24	0	0.6797	1	5

Models <sup>a</sup> by species	<i>AIC</i>	$\Delta AIC$	<i>AIC Weight</i>	<i>LogLik</i>	<i>No. Par.</i>
Indiana bat					
$\Psi$ (max temp, elevation), <i>p</i> (water)	233.25	0	0.4399	1	5
$\Psi$ (max temp, elevation, %forest), <i>p</i> (water)	235.18	1.93	0.1676	0.381	6
Evening bat					
$\Psi$ (min temp), <i>p</i> (%forest)	280.97	0	0.2297	1	4
$\Psi$ (min temp, max temp, elevation), <i>p</i> (%forest)	282.27	1.3	0.1199	0.522	6
$\Psi$ (min temp, max temp), <i>p</i> (%forest)	282.64	1.67	0.0997	0.4339	5
$\Psi$ (max temp), <i>p</i> (%forest)	282.69	1.72	0.0972	0.4232	4
$\Psi$ (.), <i>p</i> (%forest)	282.76	1.79	0.0939	0.4086	3
$\Psi$ (.), <i>p</i> (%forest, water)	282.84	1.87	0.0902	0.3926	4
Tri-colored bat					
$\Psi$ (elevation, max temp), <i>p</i> (.)	248.97	0	0.2839	1	4
$\Psi$ (elevation), <i>p</i> (.)	249.68	0.71	0.199	0.7012	3
$\Psi$ (elevation, max temp, %forest), <i>p</i> (.)	249.76	0.79	0.1912	0.6737	5

<sup>a</sup>Occupancy and detection covariates: elevation = site elevation (m); %forest = % forest in 1 km radius; water = nearest distance to water in meters; max temp=maximum temperature in degrees celsius; min temp = minimum temperature in degrees celsius; precipitation = precipitation in cm.

<sup>b</sup>When the null model was competing, this is indicated by= (.).

Table 5. Model-averaged occupancy estimates (Est.), standard errors (SE), and the lower and upper values of the 95% confidence interval range (Lower CI and Upper CI), for the top occupancy models for twelve bat species detected on the Blue Ridge Parkway, NC, USA in 2021.

Model	<i>Est.</i>	<i>SE</i>	<i>Lower CI</i>	<i>Upper CI</i>
***a Virginia big-eared bat				
$\Psi$ (.), $p$ (max temp, elevation)	0.445	0.082	0.294	0.606
*Big brown bat				
$\Psi$ (min temp), $p$ (max temp, water)	0.732	0.073	0.56	0.851
Eastern red bat				
$\Psi$ (water, min temp), $p$ (%forest)	0.624	0.094	0.418	0.787
Hoary bat				
$\Psi$ (max temp, water), $p$ (.)	0.631	0.099	0.421	0.798
Silver-haired bat				
$\Psi$ (water), $p$ (elevation)	0.49	0.099	0.304	0.673
***Gray bat				
$\Psi$ (.), $p$ (max temp)	0.233	0.102	0.09	0.484
*c Eastern small-footed bat				
$\Psi$ (.), $p$ (elevation)	0.612	0.078	0.452	0.75
**b Little brown bat				
$\Psi$ (%forest), $p$ (%forest)	0.468	0.1	0.221	0.653

Model	<i>Est.</i>	<i>SE</i>	<i>Lower CI</i>	<i>Upper CI</i>
***Northern long-eared bat				
$\Psi$ (elevation), $p$ (elevation, precipitation)	0.329	0.083	0.184	0.504
***Indiana bat				
$\Psi$ (max temp, elevation), $p$ (water)	0.366	0.109	0.175	0.592
Evening bat				
$\Psi$ (min temp), $p$ (%forest)	0.442	0.099	0.26	0.632
***Tri-colored bat				
$\Psi$ (elevation, max temp), $p$ (.)	0.462	0.123	0.233	0.691

<sup>a</sup> Three asterisks signify the species currently has a Federally Endangered conservation status.

<sup>b</sup> Two asterisks signify the species' conservation status is currently under federal review.

<sup>c</sup> One asterisk signifies the species has a conservation status listed by the state of North Carolina.

<sup>+</sup>Models did not meet goodness of fit standards ( $\hat{c} > 4$ ).

Figure 1. 2021 stationary acoustic bat survey sites at the Blue Ridge Parkway in North Carolina.

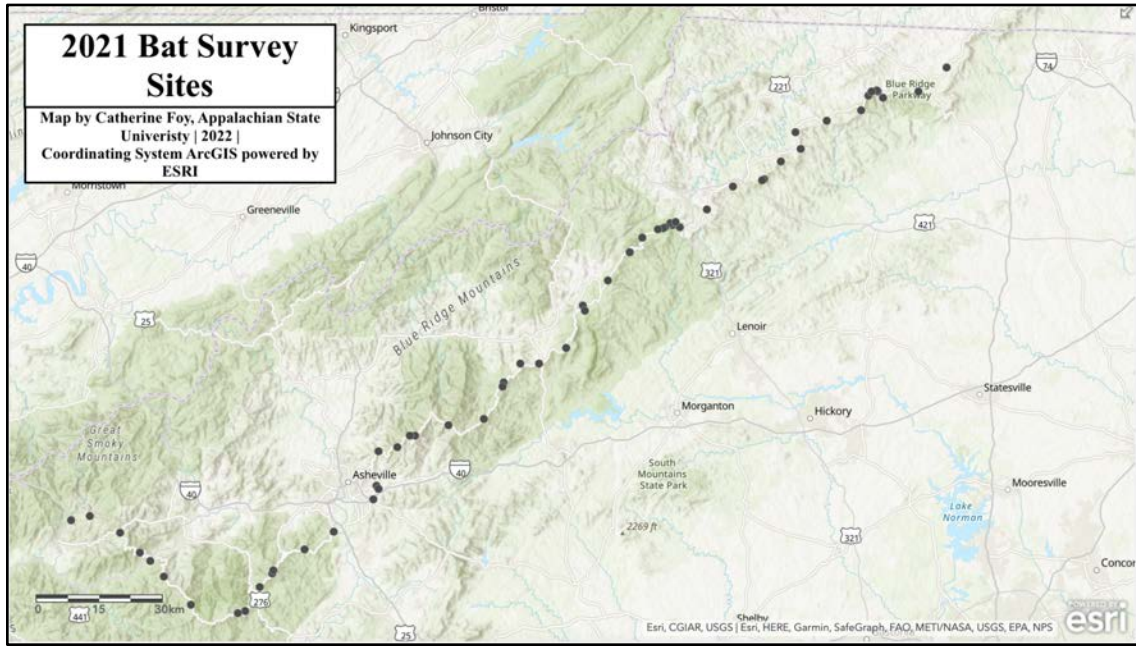


Figure 2. 2021 stationary acoustic detections of federally protected bat species at the Blue Ridge Parkway in North Carolina (sites 1-12).

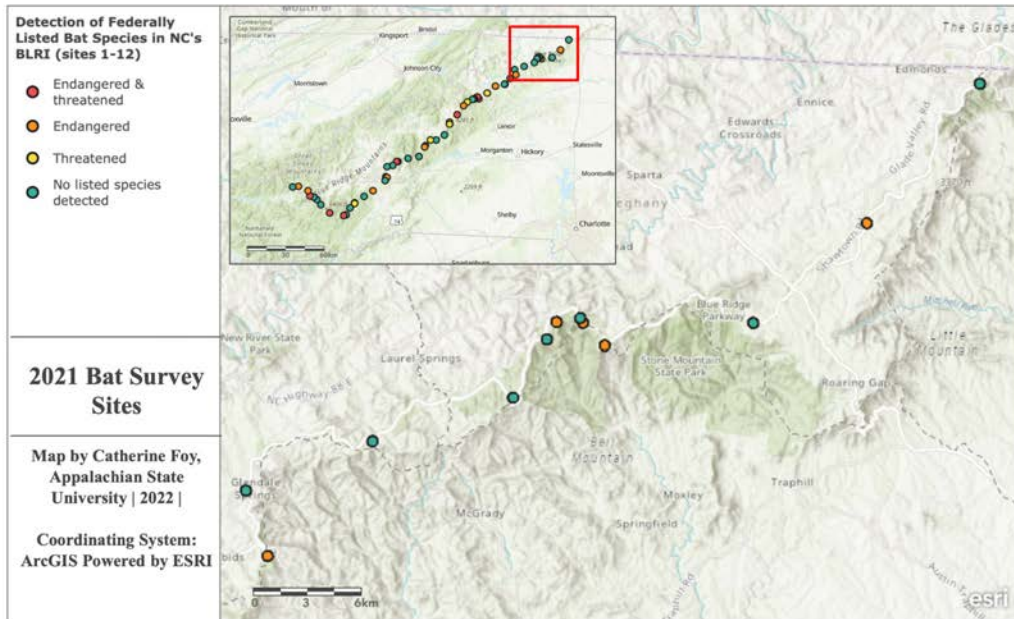
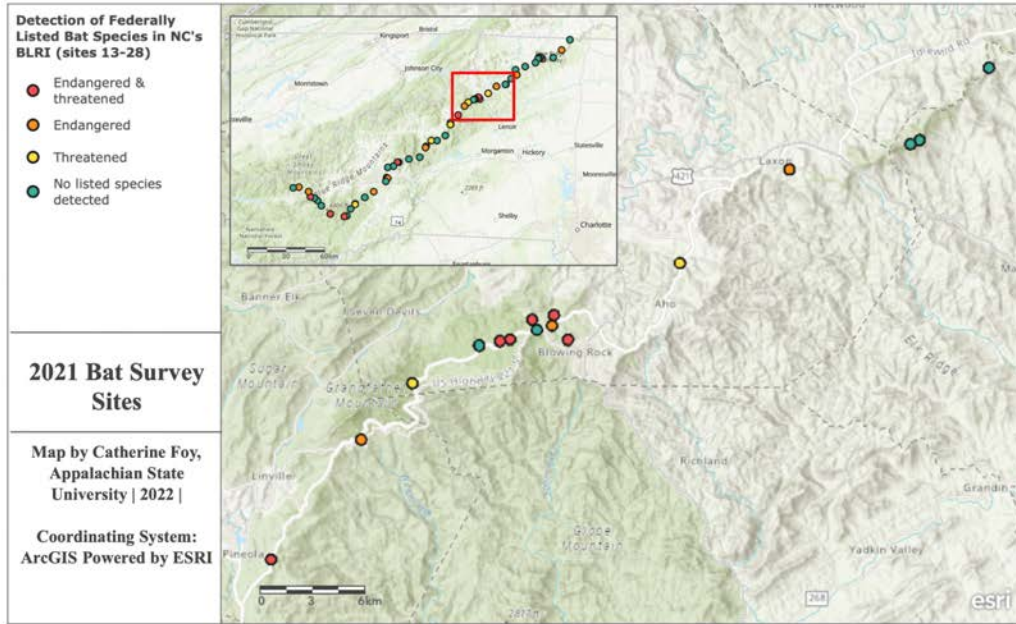


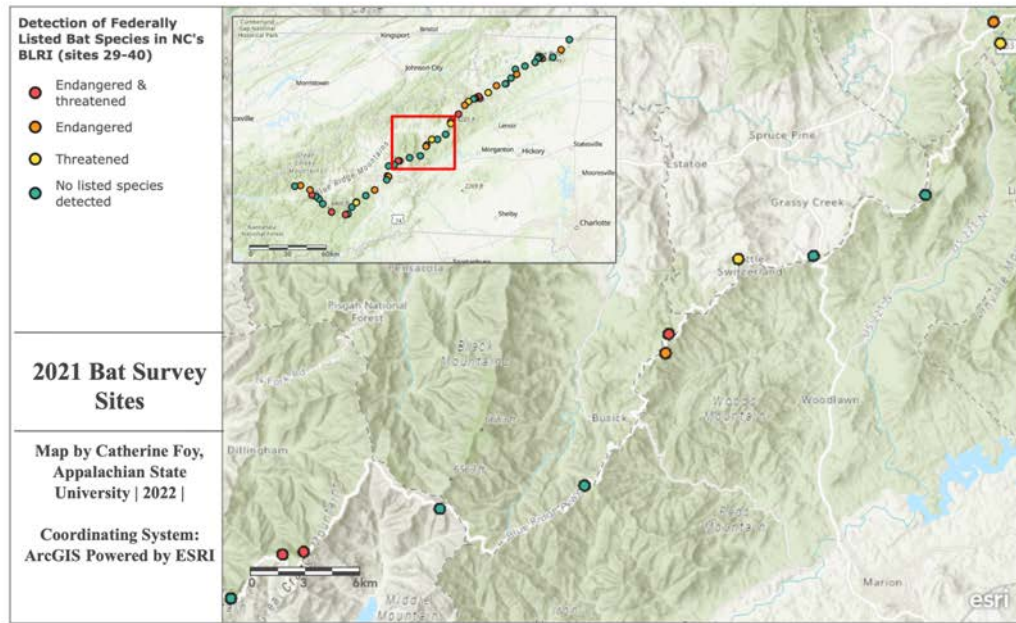


Figure 3. 2021 stationary acoustic detections of federally protected bat species at the Blue Ridge Parkway in North Carolina (sites 13-28).



Esri, NASA, NGA, USGS | State of North Carolina DOT, Esri, HERE, Garmin, SafeGraph, GeoTechnologies, Inc, METI/NASA, USGS, EPA, NPS, USDA

Figure 4. 2021 stationary acoustic detections of federally protected bat species at the Blue Ridge Parkway in North Carolina (sites 29-40).



Esri, NASA, NGA, USGS | State of North Carolina DOT, Esri, HERE, Garmin, SafeGraph, GeoTechnologies, Inc, METI/NASA, USGS, EPA, NPS, USDA

Figure 5. 2021 stationary acoustic detections of federally protected bat species at the Blue Ridge Parkway in North Carolina (sites 41-49)

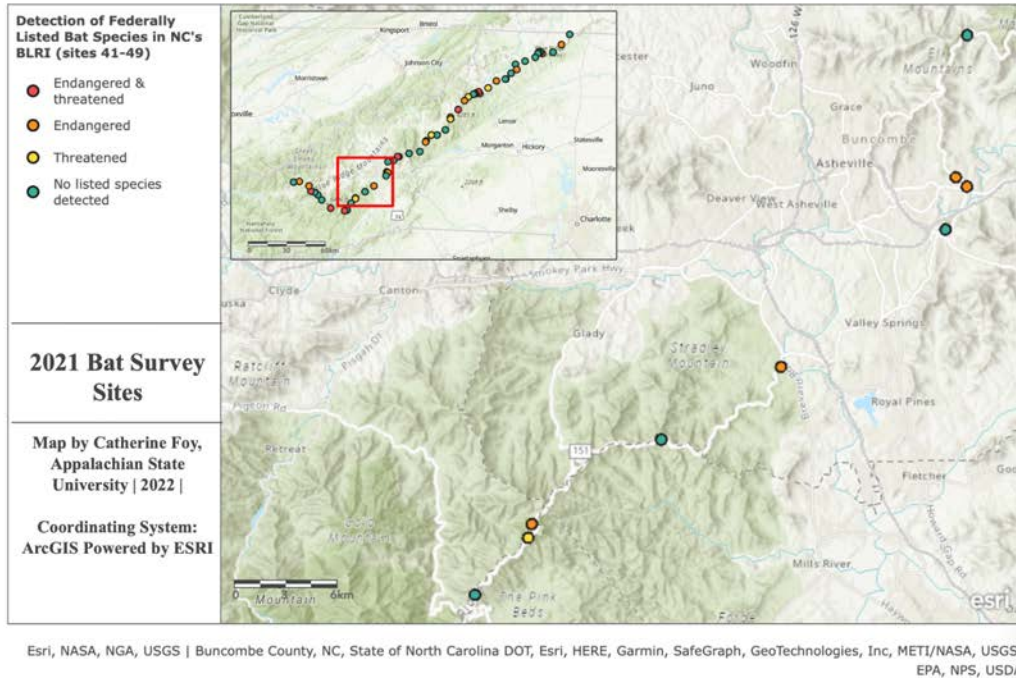


Figure 6. 2021 stationary acoustic detections of federally protected bat species at the Blue Ridge Parkway in North Carolina (sites 50-59).

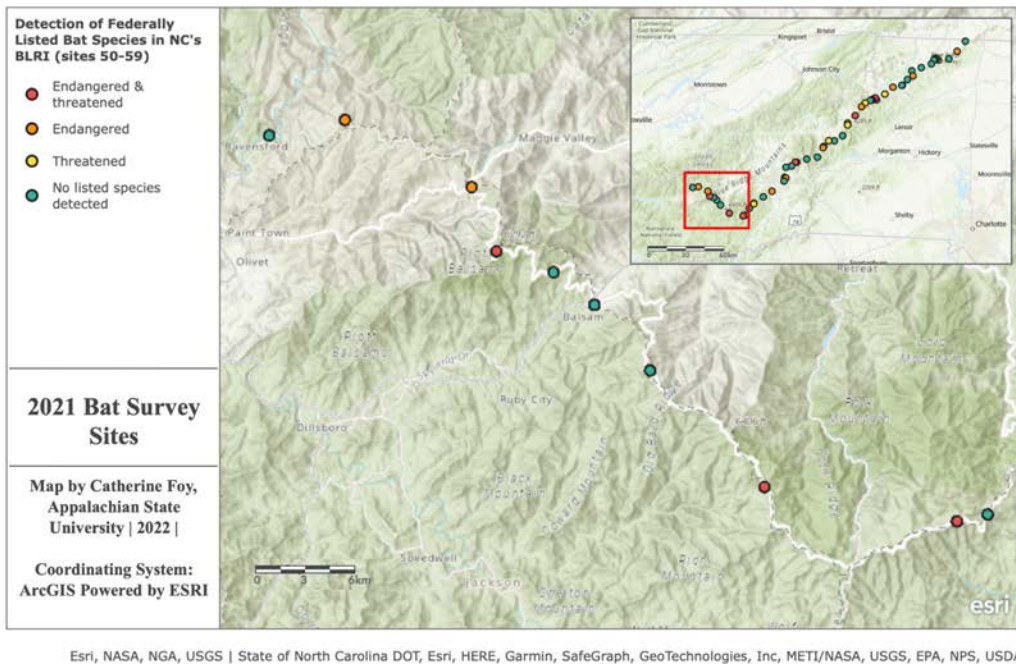
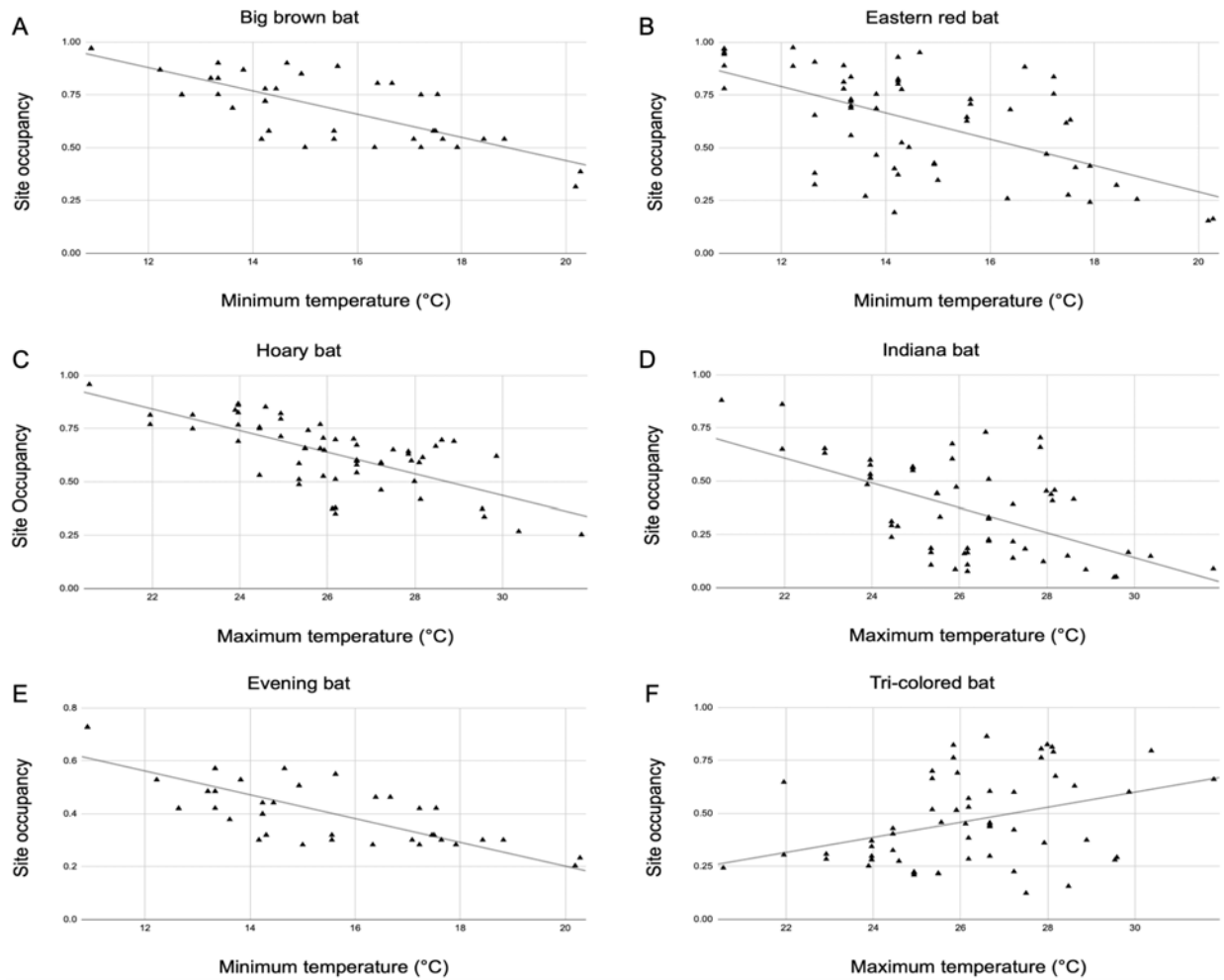




Figure 7. Six bat species modeled patterns between occupancy and minimum and maximum temperatures ( $^{\circ}\text{C}$ ; Big brown bat:  $R^2 = 0.59$ , eastern red bat:  $R^2 = 0.35$ , hoary bat:  $R^2 = 0.48$ , Indiana bat:  $R^2 = 0.32$ , evening bat:  $R^2 = 0.58$ , and tri-colored bat:  $R^2 = 0.13$ ).



## DISCUSSION

In general, the data supported my prediction that occupancy would be lower for declining and WNS susceptible species compared to those with relatively stable populations or/and those not susceptible to the disease. Occupancy results coincided with current projected population trends and conservation listings. The gray bat had the lowest site occupancy, followed by the northern long-eared bat and then the Indiana bat and all three of these species are federally endangered. The Virginia big-eared bat (federally endangered), tri-colored bat and little brown bat (both have a listing status under federal review) had low to moderate occupancy. Further, the species with relatively higher occupancy rates on the Blue Ridge Parkway were those not reported to show severe population declines: silver-haired, eastern red, hoary, and big brown bats. The evening bat and eastern small-footed bat were exceptions to these general trends. The evening bat, though considered a common species (Whitaker and Gummer 2003), had relatively low occupancy in our montane study area. Whereas the eastern small-footed bat, listed as a species of concern by the state of North Carolina (Table 1), had relatively high occupancy. Moreover, the models revealed environmental influences on occupancy for many of these species. In six species, temperature was an important predictor of occupancy while habitat variables (including elevation, distance to water and percent forest cover) predicted occupancy in some species.

There are currently seven bat species in eastern North America known to contract WNS, including: the little brown, northern long-eared, Indiana, eastern small-footed, gray, big brown and tri-colored bats (Frick et al. 2015, Table 1). Indiana and gray bats were listed as federally

endangered under the U.S. Endangered Species Act before the WNS epidemic began. The U.S. Fish and Wildlife Service listed northern long-eared bats as federally threatened in 2015 due to the risk of extinction, and unlisted the species to endangered in 2022. The Virginia big-eared bat was given Endangered Species status in 1979 because of its very limited range and declining populations. However, is not known to contract WNS. All four species of federally endangered species and the two species currently being petitioned for such protection exhibited relatively low estimates of occupancy ( $\psi$  range: 0.23 - 0.46).

As predicted, historically abundant species (the big brown, hoary, and eastern red bats) had relatively high occupancy estimates ( $\psi > 0.61$ ). However, unexpectedly, in all three of these species occupancy was higher at sites further from water and I did not see any strong negative relationships between occupancy and forested land (an expected consequence of larger bodies, less maneuverable wings, and lower frequency calls). These species are thought to forage in open areas (Morris et al. 2009) and, in South Carolina, their activity is higher over modified open water sources compared to within forest stands (Menzel et al. 2005). Certainly, water sources are important as they provide drinking and food resources for bats (Hein et al. 2008, Vindigni et al. 2009). However, most water sources on the Blue Ridge Parkway are lotic, low order streams, often within forested areas; this likely differs from those of Morris et al.'s (2009) and Menzel et al.'s (2005) field sites. Big brown bats may avoid cluttered interiors because they can maneuver and hunt more effectively in open areas while eastern red bats have intermediate maneuverability (Menzel et al. 2005, Vindigni et al. 2009). Finally, habitat-occupancy relationships for the big brown bat should be interpreted with caution as the models did not meet goodness of fit standards.

Occupancy was related to temperature for six species, and in 5 of 6 of these species, bats were more often found during times of lower temperature. The big brown, eastern red, and evening bats were found more commonly when minimum temperatures were lower and the Indiana and hoary bats were found more commonly when maximum temperature was lower (Figure 7). Minimum temperature likely corresponds to nighttime while maximum temperature corresponds to daytime. That five bat species were more commonly detected in cooler weather was unexpected as other studies demonstrate bats are more active when temperatures are higher (e.g., Erkert 1982, Erickson and West 2002). However, as temperature and elevation are difficult to disentangle (Brooks et al. 2017), it may be these relationships are driven more by higher occupancy at higher elevations. Wolbert et al. (2014) examined bat activity, insect biomass, and temperature along an elevational gradient and found the effect of temperature on bat activity depended on elevation, with temperatures having greater effects on bats at higher elevations. Further, the relationship between environmental conditions and bat activity can also depend on the study site (Martin et al. 2017). Only the tri-colored bat showed higher occupancy when maximum temperatures were higher and this trend was weak (Figure 7f). This trend was similar to that detected by Brooks et al. (2017) and is expected as insect abundance is often positively correlated with nightly ambient temperature (Agosta et al. 2003).

Although listed as a species of concern in North Carolina, and susceptible to WNS, the eastern small-footed bat had the fourth highest occupancy. Given the top model showed a positive relationship between detection and elevation, this may indicate their roosting microhabitat preferences are more common in mountainous landscapes at higher elevations. The higher elevation montane habitat on the BRP includes numerous large rocky outcrops and

crevices. These locations receive high solar exposure and are important roosting sites for reproducing eastern small-footed bat females (Erdle and Hobson 2001, Mooseman et al. 2023). High elevation rock outcrops may be a resource that attracts this species to the region and lead to higher concentrations of rare individuals.

Foraging habitat spatial complexity, or clutter (Fenton 1990) is a determining factor for bats, as morphology and echolocation capabilities affect a species' ability to hunt and navigate through spaces (Norberg and Rayner 1987, Siemers and Schnitzler 2004, Thiagavel et al. 2017). Bat echolocation calls are species-specific and context dependent, as they emit sounds in patterns tailored to the amount of acoustic 'clutter' in the environment (Broders et al. 2004, Wund 2006, Grinnell et al. 2009). Bats use a wide range of ultrasonic tonal frequencies in their calls, from ~20,000 - >200,000 Hz (Grinnell 1995). Unexpectedly, of the twelve species, the little brown bat was the only species with a top occupancy model that included percent forest. This species occurred more often in locations with less forest cover, contrary to most literature. The wings of *Myotis* species are adapted to navigate efficiently through forests (Farney and Fleharty 1969), and little brown bats have high frequency, broadband calls that echolocate efficiently in forests (Siemers and Schnitzler 2004). Patriquin et al. (2003) found *Myotis* bats were present in boreal forests; little brown bats preferred to forage along the edge of clear-cuts. Larger species, however, with lower frequency calls (big brown, hoary, eastern red, and silver-haired bats) are expected to show negative relationships between occupancy and forested land cover, as they tend to hunt in open spaces (Menzel et al. 2002). That only one species showed top models including forest cover suggests most species on the BRP forage in a diversity of Parkway habitats. It is also important to recognize the BRP sites did not include large tracts of open habitat- indeed the

percent forest cover ranged from ~48 - 96% forested. It is also possible my simple measure of percent forest does not allow for a nuanced understanding of how more complex measures of forest habitat (characteristics like size of trees, types of forest, and edge effects) influence occupancy.

Northern long-eared bats, a species that retrieves prey from surfaces such as leaves and trees, prefer to hunt in dense forest (Patriquin et al. 2003). I found elevation was the only habitat characteristic positively associated with occupancy of northern long-eared bats. Tri-colored bats were also found more often in higher elevations. This species is considered a riparian specialist, known to forage over water (Fujita and Kunz 1984, Ford et al. 2005, Kalcounis-Rueppell et al. 2007). In the BRP study area, none of the competing models for the tri-colored bat identified a correlation between occupancy and nearest distance to water. However, these models did not meet goodness of fit standards, indicating associations between occupancy and habitat should be interpreted cautiously.

Evening bats are a common species found throughout the southeastern United States (Watkins 1972). However, I found occupancy of evening bats was low and similar to that of WNS-impacted and endangered species. Although their range spans the Virginia Piedmont and Coastal Plain, there have only been two records in the Virginia mountains (Virginia Department of Wildlife Resources, 2023). Indeed, Schmidly and Bradley (2016) report evening bats inhabit elevations from sea level to 300 m. The low occupancy of this thriving species may indicate mountainous, high elevation BRP is not the preferred ecosystem for evening bats.

The advantages of passive acoustic sampling include benefits to bats (it is a less invasive survey method compared to mist netting) and benefits to researchers by reducing human effort (it allows sampling at more sites for longer periods of time). However, there are limitations to acoustic bat detector technology and the calls of some species can be difficult to discriminate. *Myotis* species might be consistently misidentified due to overlap in call characteristics (Herr 1997). The northern long-eared bat, with its low call volume, may be especially difficult to detect (Faure et al. 1993). A more thorough approach would have been to combine passive acoustic surveys with mist netting surveys to add another layer of confidence when determining species occupancy, especially when distinguishing between species belonging to the genus *Myotis*.

## MANAGEMENT IMPLICATIONS

The white-nose syndrome epidemic has decimated bat populations across North American hibernacula. Several once successful species, particularly of the genus *Myotis*, are now at risk of regional and global extinction (Frick et al. 2015, Lorch et al. 2016). By evaluating species presence and absence, we can better understand the vulnerability of each species and can make the most efficient management decisions to attenuate the impact of WNS. It is important to identify occupancy of affected species in areas where future park development is expected to take place. My data provide additional support for the observation that species hard hit by WNS have low occupancy rates. The Blue Ridge Parkway is habitat for many bat species, each with diverse adaptations and a wide range of habitat preferences and behaviors. This land provides an invaluable service, not only to bats, but to the entire ecosystem. With the ongoing threat of

WNS, conservation advocates and agencies can focus on managing land use to reduce bat species declines, especially in reducing habitat disturbance (Farrow and Broders 2011). My study should help guide conservation actions in the region, and may help mitigate further loss of bat populations and species.



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## **Vita**

Catherine Foy was accepted into the graduate program at Appalachian State University in the spring of 2021 and began study toward a Master of Science degree. In the summer of 2021 she was contracted by the National Park Service to monitor bat populations along the Blue Ridge Parkway. The M.S. was awarded in December, 2023.