Acoustic Sampling Considerations for Bats in the Post-White-nose Syndrome Landscape

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ABSTRACT

Bat populations across North America are either facing new threats from white-nose syndrome (WNS) and wind energy development or have already experienced precipitous declines. Accordingly, researchers and managers need to know how to best monitor bats to document population and distribution changes, as well as where to look for persisting populations. Landscape-scale WNS impacts to summer bat populations are not well understood, and although acoustic monitoring is commonly used to monitor these populations, there is limited information about differences among acoustic detectors and the implications to managers thereof. My objectives were to model the relationship between WNS impact, influence of available hibernacula, and environmental factors for summer nightly presence of three WNS-affected bats and to compare how multiple models of acoustic detectors perform in terms of detection probability and nightly recorded bat activity. I collected acoustic data from 10 study areas across Virginia, West Virginia, Ohio and Kentucky to describe changes in nightly presence of WNS-affected bat species during summer 2017. During the same period of time, I compared five types of acoustic detectors at Fort Knox, Kentucky. My results show the potential efficacy of using a WNS impact-year metric to predict summer bat presence, and highlight which environmental variables are relevant for large-scale acoustic monitoring. Additionally, my findings suggest that each of the detector types tested would suffice for most research and monitoring activities, but standardization of detector type within the scope of a project or study should be encouraged.

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GENERAL AUDIENCE ABSTRACT

Bat populations across North America are either facing new threats from white-nose syndrome (WNS) and wind energy development or have already experienced devastating declines. Accordingly, wildlife biologists need to know how to best monitor bats to document population and distribution changes, as well as where to look for remaining populations. Landscape-scale WNS impacts to summer bat populations are not well understood, and although acoustic technology is commonly used to monitor these populations, there is limited information about differences among acoustic detectors and the implications to managers thereof. My objectives were to model the relationship between WNS impact, influence of available bat hibernation caves, and environmental factors for summer nightly presence of three WNS-affected bats and to compare how multiple models of acoustic detectors perform in terms of detection probability and nightly recorded bat activity. I collected acoustic data from 10 study areas across Virginia, West Virginia, Ohio and Kentucky to describe changes in nightly presence of WNS-affected bat species during summer 2017. During the same period of time, I compared five types of acoustic detectors at Fort Knox, Kentucky. My results show potential viability of a WNS impact-year metric to predict summer bat presence, and highlight which environmental variables are relevant for large-scale acoustic monitoring. Additionally, my findings suggest that each of the detector types tested would suit most research and monitoring activities, but standardization of detector type within the scope of a project or study should be encouraged.

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Chapter 1: White-nose Syndrome and Environmental Correlates to Landscape-Scale Bat Presence in the Eastern United States

Abstract

Over the past 13 years, white-nose syndrome (WNS) has caused massive North American bat population declines and shifted bat community structures towards those species less or unaffected by the disease. Prior mist-netting, acoustic survey, and cave count data have been used to document changes in bat presence and activity through site-specific pre- and post- WNS studies. However, management and survey guidance often occur at a landscape scale and similarly scaled studies are needed to examine spatial as well as temporal patterns in bat presence. My objective was to model the relationship between WNS impact, influence of available hibernacula, and environmental factors for the nightly presence for three WNS-affected bats: the Indiana bat (*Myotis sodalis*), northern long-eared bat (*M. septentrionalis*), and big brown bat (*Eptesicus fuscus*). I used acoustic recordings from 10 study areas across Virginia, West Virginia, Ohio and Kentucky to describe changes in nightly bat presence during the summer of 2017. I found significant correlates of broad land cover type for presence of all three species. My findings also corroborated trends in abundance and distribution patterns found post-WNS using traditional survey techniques, supporting the relevance of coarse land cover categories in an acoustic monitoring framework for large-scale monitoring. I observed a negative association between WNS impact-years and nightly northern-long eared bat presence, but low occurrence and patchy distribution reduced my ability to infer strong relationships. Big brown bats showed a significant positive relationship with WNS occurrence on the landscape, providing more evidence that these bats are maintaining populations after years of exposure. Indiana bats were the least-documented species, limiting conclusions, but I did observe statistically

significant temporal patterns in nightly presence. My results show the potential efficacy of using a WNS impact metric to predict summer bat presence, and highlight which environmental variables are relevant for large-scale acoustic monitoring.

Introduction

Bat populations across the United States are currently experiencing extreme population declines due to the introduction and spread of the white-nose syndrome (WNS). *Pseudogymnoascus destructans* (Pd), the causative agent of WNS, is a fungus that infects the epithelial tissue of hibernating bats and leads to frequent arousal and then loss of fat reserves (Frick et al. 2010, Lorch et al. 2011). In the first six years after the disease's arrival in New York hibernacula in 2006, over six million bats died in the United States due to WNS (Coleman 2014). WNS spread to the Pacific Coast in 2016 and diseased bats now have been found in 33 states and seven Canadian provinces, and an additional five states have Pd-positive bats (Michaels 2019). Pd-caused declines are not evenly distributed across hibernating bat communities by species or geographic region. For example, cave obligate gray bats (*M. grisescens*) have shown signs of disease (Holliday 2012) but without marked population declines (Powers et al. 2016). In contrast, the USFWS listed the northern long-eared bat (*M. septentrionalis*) as threatened in 2015 due to WNS-caused declines of up to 99% across many areas of its range (50 CFR Part 17). The little brown bat (*M. lucifugus*) and tricolored bat (*Perimyotis subflavus*) are also highly affected and averaged 91% and 75% population declines in the first five years post WNS arrival, respectively (Turner et al. 2011). The endangered Indiana bat (*M. sodalis*) also shows high susceptibility to WNS (Turner et al. 2011), reversing years of population growth and potentially leading to localized extirpation in parts of its distribution (Thogmartin et al. 2012, 2013). Early in the WNS dynamic, winter cave surveys documented big brown bat (*Eptesicus fuscus)* declines in some hibernacula (Turner et al. 2011, Langwig et al. 2012). However, the species has increased in other hibernacula (Frank et al. 2014) and most summer acoustic (Brooks 2011, Ford et al. 2011) and capture surveys (Hauer et al. 2019, Huebschman 2019) indicate a stable or increasing population, perhaps due to niche release following loss of other WNS-affected species (Jachowski et al. 2014*a*). Regardless of species, bat population declines appear to be more dramatic closer to the location of and with greater time since WNS introduction (Ingersoll et al. 2016).

Counts of bats in known hibernacula provide a relatively easy assessment of cave-specific or regional winter population changes due to WNS (Ingersoll et al. 2013, Powers et al. 2015). However, Pd or WNS detection data based off of hibernacula monitoring, where the fungus is most easily documented, leads to a dataset of wintertime observations (White-Nose Syndrome Response Team 2019) that may not accurately reflect WNS impacts on summer bat populations. With the exception of the gray bat that roosts in caves year-round, most WNS-positive bat species in North America are more difficult to monitor in the summer when they disperse from caves to roost in trees, snags, emergent rock or anthropogenic structures during the maternity season (Altringham 2011). Sex, species, and region all influence widely varying seasonal migration distances; Indiana bats and little brown bats have been documented moving 14 to 557 km and 35 to 554 km, respectively (Davis and Hitchcock 1965, Britzke et al. 2006, Norquay et al. 2013, Rockey et al. 2013, Krauel et al. 2017). Additionally, individual bats from the same summer site may overwinter in different hibernacula greater than 300 km apart (Kurta and Murray 2002). As such, declines at winter hibernacula may have far-reaching, yet non-linear impacts for local populations on the summer landscape. Summer mist-net capture (Moosman et al. 2013, Huebschman 2019) and acoustic activity monitoring (Dzal et al. 2011, Ford et al. 2011, Tomás Nocera et al. 2019) studies have also documented WNS-linked declines through site-specific pre- and post-WNS longitudinal studies, albeit rather coarsely. Researchers have proposed using karst area as a proxy for measuring the number of hibernacula available to a given summer population and therefore probability of exposure to Pd (Frick et al. 2015). However, no landscape-scale research has been undertaken to compare summer bat populations across space instead of time, thereby complicating efforts to inform larger, region-wide conservation and management efforts.

Although all bat species in the temperate eastern U.S. are insectivorous, there is great diversity among species relative to foraging habitat selection. Wing loading (mass/wing area) and echolocation call structure are factors connected to foraging habitat use: bats with low wing loading and relatively high frequency calls are associated with higher clutter, whereas species with high wing loading and lower frequency calls are found in relatively open environments (Aldridge and Rautenbach 1987, Norberg and Rayner 1987). Accordingly, both capture and acoustic bat studies frequently use broad land cover categories including woodland, open water, agricultural, urban (Menzel et al. 2005*a*, Sparks et al. 2005, Johnson et al. 2008) or forest-specific categories including mature forest, thinned forest, forested riparian, forest-edge, or forest interior (Humes et al. 1999, Loeb and O'Keefe 2006, Hein et al. 2009, McGowan and Hogue 2016). Smaller-scale vegetation measurements comprising forest canopy cover, canopy height, tree density, and basal area impact local selection and activity patterns (Ford et al. 2005, Bender et al. 2015, Cox et al. 2016, Austin et al. 2019) as well as acoustic detection probability (O'Keefe et al. 2014).

Both weather and day of the year affect bat presence throughout the summer. Most cave hibernating bats arrive in forests beginning in mid- to late April, and maternity colonies form in May and June (Kurta et al. 2002). Female bats generally give birth in a window from mid-June to mid-July and newly volant juveniles for some species are captured as early as late June (Timpone et al. 2011, Francl et al. 2012, Pettit and O'Keefe 2017). As summer progresses, maternity colonies begin to disassociate and bats disperse towards hibernacula (Altringham 2011). During summer when bats are foraging or navigating, rainfall can negatively affect echolocation feedback (Griffin 1971), and bats are less likely to switch roost trees in rainy conditions (Patriquin et al. 2016). Moreover, wet bats are heavier, thereby incurring higher flight costs from an energetics standpoint (Voigt et al. 2011). Collectively, precipitation can result in an overall decrease in bat activity on the local landscape (Erickson and West 2002, Muthersbaugh et al. 2019*a*). Wind speed can also negatively affect bats, with higher wind speeds associated with a decrease in the probability of bat presence or lower activity rates due to decreases in foraging efficiency and similar energetic costs to flight (Weller and Baldwin 2012, Muthersbaugh et al. 2019*a*).

Traditionally, managers and researchers in the eastern U.S. monitored summer bat populations solely via physical capture with mist-nets. However, as ultrasonic recording technology improved, acoustic detectors have become a non-invasive and effective tool (Murray et al. 1999, O'Farrell and Gannon 1999). When designing acoustic monitoring protocols for rare or WNS-impacted species it is critical to determine optimal sampling locations based on knowledge of both bat biology and acoustic technology. As a result, current federal bat monitoring guidelines for threatened and endangered species of interest, i.e., Indiana bats and northern long-eared bats, recommend placing passive acoustic detectors away from areas of high clutter to maximize detection, and in forest openings, forest corridors, forest edges, thinned or recently logged forest, and along water sources to record a diverse species composition (Loeb et al. 2015, USFWS 2019*a*). To ensure accurate acoustic documentation of resident summer bats, both the North American Bat Monitoring Program (Loeb et al. 2015) and the USFWS Indiana Bat Summer Survey Guidance (USFWS 2019*a*) recommend sampling between June 1 and July 30, although the USFWS does allow surveys from May 15 through August 15 for regulatory clearance. Additionally, both programs only collect data from summer nights with no or minimal rainfall.

Objectives

My research goal was to examine the effectiveness of WNS impact and karst area predictors alongside commonly used landscape and site-specific variables as predictors of summer bat population presence measured by acoustic activity. To accomplish this, I examined the presence of three WNS- susceptible species: big brown bats, northern long-eared bats, and Indiana bats. To examine WNS impacts across space instead of through time at one location, and to include sites with a variety of karst landscape densities, I worked at a landscape scale and chose sites with varying times since WNS introduction and putative WNS impacts. I specifically chose to include established site-specific land cover and weather predictors that aligned with the USFWS Indiana bat summer survey and North American Bat Monitoring Program guidelines to ensure I was considering variables commonly used by land managers and to help inform future survey protocol.

I hypothesized that the summer effect of WNS would vary among the three bat species, with greater negative impact on the more vulnerable two *Myotis* species than big brown bats. Additionally, I hypothesized that probability of nightly presence would vary throughout the summer and that weather variables would influence all bat species. I expected the two forest-specialist *Myotis* species, especially the northern long-eared bat, would have greater probability of nightly presence with higher basal area and in forested canopy gaps and riparian corridors whereas big brown bats would be associated with edge and lower basal area sites.

Methods

Study Area

I conducted my acoustic study over a transect across Virginia, West Virginia, Ohio, and Kentucky. Study areas were chosen to represent the east-west spread of WNS and within the known ranges of Indiana and northern-long eared bats. I selected 10 areas, with a range of ownership and management practices, but all with diverse forest structure, riparian corridors, and open fields. These areas cover five level III ecoregions (Omernik 1987, US Environmental Protection Agency 2013) and span a linear distance of 1,000 km (Figure 1). Quantico Marine Corps Base (elev. 35 – 120 m ASL) and Fort A.P. Hill (30 – 65 m ASL) are both in the Southern Plains ecoregion, although on the border with the Piedmont, with southern mixed hardwood forests. Both Canaan Valley National Wildlife Refuge (975-1100 m ASL) and the Fernow Experimental Forest (550- 1100 m ASL) fall within the Central Appalachians, bordering the Ridge and Valley, with mesophytic Appalachian oak mixed hardwood forests at lower elevations and mixed boreal-northern hardwood forests at higher elevations. The Jug Wildlife Management Area (220 – 350 m ASL) and the Edge of Appalachia Preserve (155 – 300 m ASL) are comprised of mesophytic mixed hardwood forests and fall within the Western Allegheny Plateau. Fort Knox (135 – 250 m ASL) and the Riveroak Tract (150 – 185 m ASL) are both in the Interior Plateau with mesophytic mixed hardwood forests, although non-native loblolly pine (*Pinus taeda*) plantations comprise much of the forest at the Riveroak Tract. Clarks River National Wildlife Refuge (105 – 135 m ASL) in the Mississippi Valley Loess Plains is dominated by bottomland hardwood forest. Forested swamps and bottomland hardwood forests comprise Ballard Wildlife Management Area (95 – 120 m ASL) which falls in the Interior River Valleys and Hills ecoregion and borders the Ohio River.

Data Collection

I monitored bat presence at permanent acoustic sites from May 15 through August 15, 2017 encompassing the entire the USFWS bat summer survey sample period (U.S. Fish and Wildlife Service 2019) with Song Meter SM4BAT ZC detectors and omnidirectional SMM-U1 microphones (Wildlife Acoustics, Maynard, MA). The USFWS recommends Indiana or northern long-eared bat surveyors place detectors in any of six types of sites: (1) forest-canopy openings; (2) water sources; (3) wooded fence lines near suitable habitat; (4) recently logged forest with remaining potential roost trees; (5) wooded road or stream corridors with open canopies and (6) woodland edges (USFWS 2019*a*) . I distilled these categories into three broad types: (1) forest canopy gap or corridor; (2) forested riparian corridor and (3) forest-field edge. I placed one acoustic detector at each of three sites within the 10 study areas. Within those categories, specific detector placement sites were chosen based on accessibility and suitability for recording high-quality bat calls (i.e., minimal vegetation clutter or other obstructions and distant from known roosts). All detector sites were >80 m apart to ensure detector independence (Agranat 2014). I elevated microphones on 3 m poles and programmed detectors to record nightly from 30 minutes prior to sunset and 30 minutes after sunrise.

I identified bat calls to species using Kaleidoscope version 4.2.0 (Wildlife Acoustics, Maynard, Massachusetts) and classifier 4.2.0 at the "0" setting (USFWS 2019*b*). When analyzing calls for each study area, I included species based on prior documentation through state lists of county occurrence or from known previous mist-netting records (Francl et al. 2012, St. Germain et al. 2017, De La Cruz et al. 2018, Kentucky Department of Fish and Wildlife 2019, Virginia Department of Game and Inland Fisheries 2019). To determine nightly species presence, I used the conservative threshold set in USFWS Indiana and northern long-eared bat survey guidelines and defined probable presence at a site-night maximum likelihood estimate p-value < 0.05 from the software identifications.

At each detector site, I recorded the land cover type and examined vegetative structure and clutter via basal area and canopy closure measurements. I estimated the basal area (m^2/ha) around each microphone pole using a 20-factor prism (JIM-GEM®, Jackson, MS) and canopy closure using a concave spherical densitometer (Model-C, Forest Densiometers, Rapid City, SD**)** (Bender et al. 2015). I used Meteorological Terminal Aviation Routine records (https://mesonet.agron.iastate.edu/request/download.phtml) from the nearest airport to each study area to determine nightly rainfall amounts, which I then converted to a binary rain/no rain variable for each survey site-night.

Generating WNS and Karst maps

To understand the influence of time-since WNS and proximity to hibernacula on summer bat populations, I used available data of WNS detections and karst geology. Karst is geology with landscapes containing exposed soluble bedrock, typically limestone, and is characterized by sinkholes and caves (Ford and Williams 2013). Due to the presence of caves, which can serve as hibernacula, bats are often associated with this terrain (Furey and Racey 2016). I accessed county-level WNS detection data from the U.S. Geological Survey and Pennsylvania Game Commission (White-Nose Syndrome Response Team 2019) to generate a map of the spatiotemporal spread of WNS across the United States (Figure 2). The WNS arrival year in each county was based on the earliest date of disease detection or suspected detection (Lorch et al. 2016). I then subtracted the arrival year from the year of our survey to generate an index of WNS impact-years (e.g., I coded detection in the winter of 2010-2011 as 7 years of impact in the summer of 2017). I chose the natural neighbor raster interpolation tool (ESRI, Redlands, CA) to predict WNS impact across the U.S. because the county-level detection data was clustered and scattered (Childs 2004).

To represent potential bat winter to summer dispersal distances from hibernacula, I averaged the WNS impact-years within 50, 100, and 150 km buffers. I calculated the percent of karst area in each buffer to represent the amount of potentially available hibernacula around summer sites (Frick et al. 2015, Christman et al. 2016) using spatial data from Tobin and Weary (2004) within the same three buffer sizes.

Data Analysis

To examine the relationship between nightly Indiana, northern long-eared, and big brown bat presence, WNS impact-years, amount of available or potential hibernacula, and established weather and land cover predictors (Table 1), I developed a set of species-specific *a priori* candidate models. I modeled nightly bat presence for each species using binary-response generalized linear mixed models (GLMMs) in program R version 3.6.0 (R Core Team 2019) with package glmmTMB (Brooks et al. 2017) with nested random effects to account for spatial auto-correlation of the three sampling sites within each of the 10 larger study areas. I used a two-step information theoretic approach in building the candidate models with Akaike's Information Criterion corrected for small sample size (AICc from package bbmle, Bolker 2017; Burnham and Anderson 2002) to rank models and then considered best supported models with a ΔAICc < 2.

I initially used model ranking to determine the best-fitting date structure and buffer size from both WNS impact-years and karst area best supported models and then combined them with weather and vegetation data to build final comprehensive model sets. To determine the most species-appropriate WNS impact-year and karst area buffers, I ran GLMMs for each bat species and covariate type and then selected the best-performing buffers. To account for potential nonlinear changes in probability of nightly bat presence over the summer survey period, I compared GLMMs with different polynomial structures on date for each species and selected the best-performing date structure. Prior to building final model sets, I assessed potential correlation among continuous predictors using package corrplot (Wei and Simko 2017) in program R version 3.6.0 (R Core Team 2019) to ensure that highly correlated ($r \geq 0.6$) variables were not included in the same model. Canopy cover was highly correlated with basal area and accordingly these covariates were not modeled together. All continuous predictors were centered and scaled prior to analysis (Schielzeth 2010).

Lastly, after building final candidate model sets, I used the same information theoretic approach to rank models for the separate nightly Indiana, northern long-eared, and big brown bat presence data. Of the 10 study areas, the Quantico Marine Corps Base study area was outside of the documented Indiana bat maternity colony range (USFWS 2015, St. Germain et al. 2017), therefore I removed it from Indiana bat analyses.

Results

During the summer of 2017, I sampled 2,430 site-nights across 30 survey-sites collectively over all 10 areas for northern long-eared bats and big brown bats and 2,252 nights across 27 sites over 9 of the areas for Indiana bats (Table 2). A staggered deployment across four states and two detector failures led to uneven sampling periods among sites. Over the entire effort, Kaleidoscope identified 249,990 call files to bat species.

WNS and Karst results

Study areas varied in WNS impact-years. I calculated 3.1 years of impact in western Kentucky and 3.7 years of impact in the northwestern West Virginia site. Both Virginia sites and the mountainous sites in east-central West Virginia had highest WNS-impact years with values ranging from 7.8 to 6.6. The amount of karst landscape also varied among study areas. Central

Kentucky buffers contained up to 76% karst area, whereas the Virginia and northwestern West Virginia sites had only 0.05 to 0.15% karst area.

Indiana bat

I recorded Indiana bat presence at 24 out of 27 sites where it potentially could occur and for 254 nights out of 2,252 site-nights. There were seven competing models within two AICc units of the best supported model (Table 3). The most parsimonious competing model was the date-only model with a 3rd order polynomial term. Indiana bat presence was highest in early June, and then declined throughout the summer until an upward trend in mid-August (Figure 3). Although adding land cover minimally improved the model ranking, it was the only other significant variable among the seven competing models. Indiana bats were significantly more likely to be present in forested riparian corridors than in forest-field edges (Table 4).

Northern long-eared bat

I recorded northern long-eared bat presence at 19 out of 30 sites and for 321 nights out of 2,430 site-nights. There were eight competing models within two AICc of the best supported model (Table 3). The best supported and most parsimonious model contained date and land cover, although the model adding a 50 km WNS impact year buffer was within 0.04 AIC units of the best supported model. Land cover type was the only statistically significant variable among all competing models (Table 5). Northern long-eared bats were more likely to be present in forest and riparian sites than forest-field edge sites. Although the years of WNS impact variable was not statistically significant, 65% of all northern long-eared bat detections were at the two study areas with less than four years of WNS impact (Figure 4).

Big brown bat

I recorded big brown bat presence at 29 out of 30 sites and for 725 nights out of 2,430 site-nights. There were two competing models within two AICc of the best supported model. The best supported and most parsimonious model contained a 3rd order polynomial on date, land cover type, and the 150 km buffers for both WNS impact-years and proportion of karst (Table 3). Big brown bats were significantly less likely to be present in forest and riparian sites than edge sites, although the effect size for riparian sites was smaller, and significantly more likely to be present at sites with greater karst area and WNS impact-years in 150km buffers (Table 6). The probability of detecting big brown bat presence varied across the summer. Probability of detection decreased from mid-May through mid-June, and then increased until a peak in late July (Figure 6).

Discussion

This large, landscape study provided an opportunity to examine a myriad of fine, broad, and landscape-level influences on WNS-impacted bat populations. Consistent with my expectations, nightly bat presence across the study area varied by the three species examined, with time over the summer survey period and generally tied to broad-scale land cover categories. Most northern long-eared bat presences were documented at study areas with the fewest WNS impact-years. Contrary to my expectation, I observed more big brown bats at older WNS impact areas, supporting the recent observations of Deeley (2019) that big brown bat activity and capture rates increased post-WNS. However, I did not find support for basal area, a finer-scale vegetation structure measure and surrogate for forest clutter, or nightly precipitation as useful predictors of nightly bat presence across this long term and large-scale acoustic bat survey. Overall, the WNS impact-year metric I developed showed some utility, and could help identify areas with likely remnant populations of WNS-impacted bats, such as The Jug WMA.

My results suggest that for all three species, broad categorization of vegetation structure or land cover type is a useful predictor of site-specific presence. Both northern long-eared and Indiana bats were more likely to be found in forested riparian corridors than forest-field edge sites, whereas northern long-eared bats were also more likely to be found in forested corridors and canopy gaps than forest-field edges. This aligned with my initial predictions that *Myotis* species with more maneuverability to navigate forested areas and glean prey off of vegetation would be found in forest-interior sites (Patriquin and Barclay 2003, Lacki et al. 2007, Starbuck et al. 2015). Riparian areas are important for bat foraging (Grindal et al. 1999, Jachowski et al. 2014*b*) due to the abundance of insect prey (Fukui et al. 2006) and also serve as a water source (Seibold et al. 2013). Acoustic surveys have consistently documented the importance of forested riparian areas, particularly relatively closed forests, for both northern long-eared and Indiana bats (Owen et al. 2004, Schirmacher et al. 2007, Johnson et al. 2010) and this pattern was consistent across my large overall study areas. Conversely, as expected, big brown bat presence was less likely at forested riparian corridors and forest corridors than at forest-field edge sites. Larger bodied, less maneuverable bats including the big brown bat use open areas more than cluttered, interior forests (Brooks and Ford 2005, Ford et al. 2005). The persistence of these trends across a landscape-scale study emphasizes the importance of forest-field edges (Wolcott and Vulinec 2012, Jantzen and Fenton 2013) and forested riparian corridors (Owen et al. 2004) and the need to maintain a diverse landscape.

For all species, finer scale vegetation measurements and precipitation had no measurable effect on nightly presence. I expected basal area to be relevant for nightly presence, because increasing basal area has been linked to a decrease in detection for some less clutter adapted species (Bender et al. 2015) and the opposite is true for clutter adapted species (Blakey et al. 2019). However, other acoustic studies have documented a similar lack of relationship between basal area and bat detection (Hein et al. 2009). Precipitation often has a negative impact on nightly bat activity and detection (Erickson and West 2002, Yates and Muzika 2006, Muthersbaugh et al. 2019*b*), however in this study, I generally found no effect. Bats are known to forage in light rain (Erkert 1982) and only delayed emergence minimally when rain noises were played outside roosts (Geipel et al. 2019). Austin et al. (2019) similarly found no relationship between precipitation and bat detection, indicating that precipitation may have more of an impact on bat activity than presence or detection.

Consistent with my expectation, date had a significant effect on the probability of bat presence throughout the summer survey period. I observed an increase in the probability of big brown bat presence later in the summer, peaking in mid- July, which could be consistent with successful reproduction and subsequent addition of newly volant juveniles to the landscape (Ford et al. 2011, Tomás Nocera et al. 2019) or lactating females increasing localized foraging effort to support higher energetic demands of nursing pups (Deeley 2019). There is evidence that big brown bats may maintain similar levels of reproductive output post-WNS (Francl et al. 2012) and thus pre-WNS trends persist. Conversely, the trend for probability of Indiana bat presence was lower in the second half of the summer; however, the overall probability remained relatively low throughout the entire survey period. Overall, Indiana bat activity declines after WNS, but no changes to the within-summer patterns have been documented between pre- and post-WNS acoustic survey datasets in the Northeast (Ford et al. 2011, Nocera et al. 2019). In a post-WNS landscape, overall Indiana bat capture rates decline, but the proportion of non-reproductive adult female captures increases, perhaps indicating that fewer WNS-affected individuals are able to reproduce (Pettit and O'Keefe 2017).

My results were partially consistent with the hypothesis that *Myotis* species presence would show a negative response to increased years of WNS impact. I documented the majority of northern long-eared bats at the two study areas with less than four WNS impact-years. Bat populations decline rapidly for two-four years after WNS detection and may stabilize at low levels (Langwig et al. 2012) which supports the accuracy of my WNS impact-year calculation and explains the rapid decline in nightly northern long-eared bat presence after between three and four WNS impact-years. There was an unexpected small increase in northern long-eared bat presence at the higher end of the WNS impact-year scale, potentially explaining why the variable was not significant in the overall model. Two of the sites with > 7 WNS impact-years were in eastern Virginia, an area with no natural hibernacula to survey and limited WNS documentation (White-Nose Syndrome Response Team 2019). The low resolution of data points in central and eastern Virginia may have limited my WNS impact interpolation, thus limiting the conclusions. However, coastal populations of northern long-eared bats in nearby northeastern North Carolina (Grider et al. 2016) and also in coastal Massachusetts (Dowling and O'Dell 2018) continue to persist despite documented WNS in those states. Without natural hibernacula close-by, these surviving bats overwinter in houses (Dowling and O'Dell 2018) and trees, and with only periodic bouts of torpor, leave roosts to forage and have the ability to groom (Hawkins et al. 2017), thus limiting WNS exposure and impact. As a result, the WNS impact-years metric may not be as relevant in coastal areas where northern long-eared bats may use alternative hibernacula.

Unexpectedly, I found no relationship between WNS impact and Indiana bat presence. This does not align with prior site-specific pre and post-WNS summer studies that show activity rate declines in New York through acoustic monitoring (Ford et al. 2011, Tomás Nocera et al. 2019), and capture rate declines in Wisconsin (Huebschman 2019), Indiana (Pettit and O'Keefe 2017) and West Virginia (Francl et al. 2012). This discrepancy may be a result of the fact that Indiana bats were the least-documented of the three species that I examined and were considered rare on the landscape even prior to the advent of WNS. Although Indiana bat winter hibernacula are monitored with biennial surveys (USFWS 2009), summer populations are difficult to find, in fact, it is estimated that only 10% of extant maternity colonies relative to known overwintering populations have been documented (USFWS 2009). My landscape-scale study may not have been detailed or targeted enough to document the association between WNS and summer Indiana bat populations that exist at low densities.

I found that both greater WNS impact-years and percent karst area were associated with a higher probability of big brown bat presence. The relationship between my WNS impact metric and big brown bat presence is consistent with summer work documenting capture rate increases of 17% from pre to 1-year post WNS in West Virginia (Francl et al. 2012) and 12% from pre to 2-3 years post WNS in Indiana (Pettit and O'Keefe 2017). Big brown bats show a resistance to WNS, potentially due to their larger body size and associated higher fat stores (Frank et al. 2014). It follows that these less-impacted bats would still be prevalent and associated with areas with more potential hibernacula if they are not negatively affected by WNS in these areas. Big brown bat increases in a post-WNS summer landscape could be tied to a reduction in interspecies competition, whereby optimal foraging habitat is more available to the remaining individuals (Jachowski et al. 2014*a*). However, despite an overall increase in big brown bat capture rates, the proportion of reproductive females captured decreased post-WNS in Indiana (Pettit and O'Keefe 2017). Although these data support a broad-scale increase in big brown bat presence post-WNS there may be site-specific factors contributing to local population changes.

Survey Implications

Overall, I detected far fewer *Myotis* species than big brown bats, reinforcing the fact that remaining individuals in WNS–impacted populations are now even more patchily distributed on the landscape. Even with this limited dataset, I documented low WNS impact sites in Kentucky and West Virginia with potential residual northern long-eared bat colonies. My WNS impact map could serve as a tool to guide future summer monitoring efforts by highlighting those areas with a greater likelihood to host remaining northern long-eared bat populations or at minimum provide areas where remaining natural history and ecology information about the species can be obtained prior to WNS caused declines (Hyzy et al. in press). Given the rarity of *Myotis* species across the landscape, summer sampling needs to be optimized to maximize chances of detection when actually present. Forest-field edge sites are important to include in sampling when the goal is to document a wide range of species, such as in the North American Bat Monitoring Program. However, when the goal is to document presence or absence of northern long-eared or Indiana bats, edge or open sites should be minimized in favor of forested corridors, canopy gaps, and riparian corridors. In these forested environments, clutter may not be a determinant for documenting presence. Once researchers follow best practices for deploying acoustic detectors and avoid areas of dense clutter that would affect recordings, land cover or other larger scale predictors may be more relevant.

In light of my results, current standards that allow up to 30 minutes of rain (USFWS 2019*a*) for Indiana bat presence surveys or little or no rain for North American Bat Monitoring Program surveys (Loeb et al. 2015) may be conservative, but undoubtedly help minimize the risk of false negative results. Longer-term surveys with many nights at each site may not need the same level of caution. Additionally, sampling for summer presence as late as August 15th as accepted in current standards may be too late for some areas where maternity colony formation, parturition, juvenile volancy and colony disaggregation occur earlier rather than later. Although I had a small number of detections, the decline in probability of nightly Indiana bat presence later in the summer aligns with other work (Francl et al. 2012, Pettit and O'Keefe 2017), possibly documenting a shift in reproduction that could shift the ideal survey window earlier. From my results, for example, ending the survey period at the end of July may have conveyed the same information as continuing work through mid-August. This study provides some support for my WNS impact - year metric, but I was limited by only having sites with three to eight impact-years and already declining *Myotis* populations. Once the four WNS impact-year threshold was crossed, there was no discernable effect of WNS impact-years on nightly northern long-eared bat presence. More sites or sites in non-WNS impacted areas could have increased robustness and potentially improved model performance. Additionally, this study adds more evidence to support the conclusion that northern long-eared bats in coastal areas without traditional hibernacula do not follow the expected population decline patterns. More year-round study is needed in coastal areas without associated karst landscapes to understand WNS-impacted populations. Critically, more monitoring is needed prior to WNS impacts as the Pd fungus spreads west across North America.

Literature Cited

Adams, A. M., M. K. Jantzen, R. M. Hamilton, and M. B. Fenton. 2012. Do you hear what I hear? Implications of detector selection for acoustic monitoring of bats. Methods in Ecology and Evolution 3:992–998.

Agranat, I. 2014. Detecting bats with ultrasonic microphones: Understanding the effects of microphone variance and placement on detection rates. Wildlife Acoustics, Inc., Maynard, MA. <https://www.wildlifeacoustics.com/images/pdfs/UltrasonicMicrophones.pdf>.

Aldridge, H. D. J. N., and I. L. Rautenbach. 1987. Morphology, echolocation and resource partitioning in insectivorous bats. Journal of Animal Ecology 56:763–778.

Altringham, J. D. 2011. Bats: From Evolution to Conservation. OUP Oxford.

Arnett, E. B., and E. F. Baerwald. 2013. Impacts of wind energy development on bats: implications for conservation. Pages 435–456 *in* R. A. Adams and S. C. Pedersen, editors. Bat Evolution, Ecology, and Conservation. Springer New York.

Arnett, E. B., M. M. Huso, M. R. Schirmacher, and J. P. Hayes. 2011. Altering turbine speed reduces bat mortality at wind-energy facilities. Frontiers in Ecology and the Environment 9:209–214.

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 38:183–195.

Austin, L. V., A. Silvis, W. Mark Ford, and K. E. Powers. 2019. Effects of historic wildfire and prescribed fire on site occupancy of bats in Shenandoah National Park, Virginia, USA. Journal of Forestry Research 1–16.

Bender, M. J., S. B. Castleberry, D. A. Miller, and T. Bently Wigley. 2015. Site occupancy of foraging bats on landscapes of managed pine forest. Forest Ecology and Management 336:1–10.

Blakey, R. V., E. B. Webb, D. C. Kesler, R. B. Siegel, D. Corcoran, and M. Johnson. 2019. Bats in a changing landscape: Linking occupancy and traits of a diverse montane bat community to fire regime. Ecology and Evolution 9:5324–5337.

Bolker, B. 2017. Tools for General Maximum Likelihood Estimation. <https://cran.r-project.org/web/packages/bbmle/bbmle.pdf>. Accessed 10 Aug 2019.

Britzke, E. R., A. C. Hicks, S. L. Von Oettingen, and S. R. Darling. 2006. Description of spring roost trees used by female Indiana bats (*Myotis sodalis*) in the Lake Champlain Valley of Vermont and New York. The American Midland Naturalist 155:181–187.

Britzke, E. R., B. A. Slack, M. P. Armstrong, and S. C. Loeb. 2010. Effects of orientation and weatherproofing on the detection of bat echolocation calls. Journal of Fish and Wildlife Management 1:136–141.

Broken-Brow, J. 2018. AnaBat Swift bat detector user manual. User Manual, Titley Scientific, Columbia, Missouri, USA.

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker. 2017. Modeling zero-inflated count data with glmmTMB. bioRxiv 132753.

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

Brooks, R. T., and W. M. Ford. 2005. Bat activity in a forest landscape of central Massachusetts. Northeastern Naturalist 12:447–462.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Springer, New York, NY.

Childs, C. 2004. Interpolating Surfaces in ArcGIS Spatial Analyst. ArcUser July-September:32–35.

Christman, M. C., D. H. Doctor, M. L. Niemiller, D. J. Weary, J. A. Young, K. S. Zigler, and D. C. Culver. 2016. Predicting the occurrence of cave-inhabiting fauna based on features of the earth surface environment. PLOS ONE 11:e0160408.

Coleman, J. 2014. White-Nose Syndrome The devastating disease of hibernating bats in North America. US Fish & Wildlife Publications. <https://digitalcommons.unl.edu/usfwspubs/453>.

Coleman, L. S., W. M. Ford, C. A. Dobony, and E. R. Britzke. 2014. A comparison of passive and active acoustic sampling for a bat community impacted by White-nose Syndrome. Journal of Fish and Wildlife Management 5:217–226.

Cox, M. R., E. V. Willcox, P. D. Keyser, and A. L. Vander Yacht. 2016. Bat response to prescribed fire and overstory thinning in hardwood forest on the Cumberland Plateau, Tennessee. Forest Ecology and Management 359:221–231.

Cranfill, R. 1991. Flora of Hardin County, Kentucky. Castanea 56:228–267.

D500X user’s manual. 2017. User Manual, Pettersson Elektronik AB, Uppsala, Sweden.

Davis, W. H., and H. B. Hitchcock. 1965. Biology and Migration of the Bat, Myotis lucifugus, in New England. Journal of Mammalogy 46:296–313.

De La Cruz, J., R. L. Ward, and E. S. Schroder. 2018. Landscape characteristics related to use of artificial roosts by northern long-eared bats in north-central West Virginia. Northeastern Naturalist 25:487–501.

Deeley, S. 2019. Ecology of mid-Atlantic bats post-WNS: Communities, diet, and reproduction along an urban-to-rural gradient. Dissertation, Virginia Polytechnic Institute and State University, Blacksburg, VA, USA.

Dowling, Z. R., and D. I. O'Dell. 2018. Bat Use of an Island off the Coast of Massachusetts. Northeastern Naturalist 362–382.

Duchamp, J. E., M. Yates, R.-M. Muzika, and R. K. Swihart. 2006. Estimating probabilities of detection for bat echolocation calls: an application of the double-observer method. Wildlife Society Bulletin 34:408–412.

Dyer, J. M. 2006. Revisiting the deciduous forests of eastern North America. BioScience 56:341–352.

Dzal, Y., L. P. McGuire, N. Veselka, and M. B. Fenton. 2011. Going, going, gone: the impact of white-nose syndrome on the summer activity of the little brown bat (Myotis lucifugus). Biology Letters 7:392–394.

Erickson, J. L., and S. D. West. 2002. The influence of regional climate and nightly weather conditions on activity patterns of insectivorous bats. Acta Chiropterologica 4:17–24.

Erickson, J. L., and S. D. West. 2003. Associations of bats with local structure and landscape features of forested stands in western Oregon and Washington. Biological Conservation 109:95–102.

Erkert, H. G. 1982. Ecological Aspects of Bat Activity Rhythms. Pages 201–242 *in* T. H. Kunz, editor. Ecology of Bats. Springer US, Boston, MA. <https://doi.org/10.1007/978-1-4613-3421-7_5>. Accessed 9 Sep 2019.

Fenton, M. B., S. Bouchard, M. J. Vonhof, and J. Zigouris. 2001. Time-expansion and zero-crossing period meter systems present significantly different views of echolocation calls of bats. Journal of Mammalogy 82:721–727.

Fiske, I., and R. Chandler. 2011. unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Ford, D., and P. Williams. 2013. Introduction to Karst. Pages 1–8 *in*. Karst Hydrogeology and Geomorphology. John Wiley & Sons, Ltd. <https://onlinelibrary.wiley.com/doi/abs/10.1002/9781118684986.ch1>. Accessed 28 Oct 2019.

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 2:125–134.

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 126:528–539.

Francl, K. E., W. M. Ford, D. W. Sparks, and V. Brack. 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 3:33–42.

Frank, C. L., A. Michalski, A. A. McDonough, M. Rahimian, R. J. Rudd, and C. Herzog. 2014. The resistance of a North American bat species (Eptesicus fuscus) to white-nose syndrome (WNS). PLoS ONE 9:e113958.

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 329:679–682.

Frick, W. F., S. J. Puechmaille, J. R. Hoyt, B. A. Nickel, K. E. Langwig, J. T. Foster, K. E. Barlow, T. Bartonička, D. Feller, A.-J. Haarsma, C. Herzog, I. Horáček, J. van der Kooij, B. Mulkens, B. Petrov, R. Reynolds, L. Rodrigues, C. W. Stihler, G. G. Turner, and A. M. Kilpatrick. 2015. Disease alters macroecological patterns of North American bats. Global Ecology and Biogeography 24:741–749.

Fukui, D., M. Murakami, S. Nakano, and T. Aoi. 2006. Effect of emergent aquatic insects on bat foraging in a riparian forest. Journal of Animal Ecology 75:1252–1258.

Furey, N. M., and P. A. Racey. 2016. Conservation Ecology of Cave Bats. Pages 463–500 *in* C. C. Voigt and T. Kingston, editors. Bats in the Anthropocene: Conservation of Bats in a Changing World. Springer International Publishing, Cham. <https://doi.org/10.1007/978-3-319-25220-9_15>. Accessed 28 Oct 2019.

Geipel, I., M. J. Smeekes, W. Halfwerk, and R. A. Page. 2019. Noise as an informational cue for decision-making: the sound of rain delays bat emergence. Journal of Experimental Biology 222:jeb192005.

Grider, J. F., A. L. Larsen, J. A. Homyack, and M. C. Kalcounis-Rueppell. 2016. Winter activity of coastal plain populations of bat species affected by white-nose syndrome and wind energy facilities. PLoS One 11:e0166512.

Griffin, D. R. 1971. The importance of atmospheric attenuation for the echolocation of bats (Chiroptera). Animal Behaviour 19:55–61.

Grindal, S. D., J. L. Morissette, and R. M. Brigham. 1999. Concentration of bat activity in riparian habitats over an elevational gradient. Canadian Journal of Zoology 77:972–977.

Hauer, C., L. Powers, D. Mcnaughton, C. Paul, and B. Sewall. 2019. Changes in a summer bat community in southeastern Pennsylvania. Journal of the Pennsylvania Academy of Science 93:47–62.

Hawkins, J. A., M. K. Gooden, G. G. Janos, and P. L. Sewell. 2017. Fall 2016/Winter 2017 NCDOT Northern Long-eared Bat Research Project, Bertie, Bladen, Hyde, Martin, and Tyrrell Counties, North Carolina. Copperhead Environmental Consulting, INC., Paint Lick, Kentucky.

Hein, C. D., S. B. Castleberry, and K. V. Miller. 2009. Site-occupancy of bats in relation to forested corridors. Forest Ecology and Management 257:1200–1207.

Holliday, C. 2012. 2012 White-nose Syndrome disease surveillance and bat population monitoring report: A report of the Tennessee WNS Response Cooperators. Tennessee Chapter of The Nature Conservancy. <http://www.tnbwg.org/2012%20White%20Nose%20Syndrome%20Report.pdf>. Accessed 2 Oct 2019.

Hourigan, C., and C. Corben. 2012. AnaBat SD2 compact flash detector user manual. User Manual, Titley Scientific, Columbia, Missouri, USA.

Huebschman, J. J. 2019. Bats in southwest Wisconsin during the era of white-nose syndrome. Northeastern Naturalist 26:168–182.

Humes, M. L., J. P. Hayes, and M. W. Collopy. 1999. Bat activity in thinned, unthinned, and old-growth forests in western Oregon. The Journal of Wildlife Management 63:553–561.

Hyzy, B. A., R. E. Russell, A. Silvis, W. M. Ford, J. Riddle, and K. Russel. In press. Investigating maternity roost selection of northern long-eared bats at three sites in Wisconsin. Endangered Species Research.

Ingersoll, T. E., B. J. Sewall, and S. K. Amelon. 2013. Improved analysis of long-term monitoring data demonstrates marked regional declines of bat populations in the eastern United States. PLoS ONE 8:e65907.

Ingersoll, T. E., B. J. Sewall, and S. K. Amelon. 2016. Effects of white-nose syndrome on regional population patterns of 3 hibernating bat species. Conservation Biology 30:1048–1059.

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

Jachowski, D. S., J. B. Johnson, C. A. Dobony, J. W. Edwards, and W. M. Ford. 2014*b*. Space use and resource selection by foraging Indiana bats at the northern edge of their distribution. Endangered Species Research 24:149–157.

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

Johnson, J. B., J. W. Edwards, and W. M. Ford. 2011. Nocturnal activity patterns of northern myotis (Myotis septentrionalis) during the maternity season in West Virginia (USA). Acta Chiropterologica 13:391–397.

Johnson, J. B., W. M. Ford, J. W. Edwards, and M. A. Menzel. 2010. Bat community structure within riparian areas of northwestern Georgia, USA. Folia Zoologica 59:192–202.

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.

Kaiser, Z. D. E., and J. M. O'Keefe. 2015. Data acquisition varies by bat phonic group for 2 types of bat detectors when weatherproofed and paired in field settings. Wildlife Society Bulletin 39:635–644.

Kentucky Department of Fish and Wildlife. 2019. Bats of Kentucky. <https://fw.ky.gov/Wildlife/Pages/Bats-of-Kentucky.aspx>. Accessed 30 Oct 2019.

Krauel, J. J., L. P. McGuire, and J. G. Boyles. 2017. Testing traditional assumptions about regional migration in bats. Mammal Research 1–9.

Kubista, C., and A. Bruckner. 2017. Within-Site Variability of Field Recordings from Stationary, Passively Working Detectors. Acta Chiropterologica 19:189–197.

Kurta, A., and S. W. Murray. 2002. Philopatry and migration of banded Indiana bats (*Myotis sodalis*) and effects of radio transmitters. Journal of Mammalogy 83:585–589.

Kurta, A., S. W. Murray, and D. H. Miller. 2002. Roost selection and movements across the summer landscape. Pages 118–129 *in* A. Kurta and J. Kennedy, editors. The Indiana bat: biology and management of an endangered species. Bat Conservation International, Austin, Texas, USA.

Lacki, M. J., J. P. Hayes, and A. Kurta. 2007. Bats in forests: Conservation and management. JHU Press.

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

Law, B., L. Gonsalves, P. Tap, T. Penman, and M. Chidel. 2015. Optimizing ultrasonic sampling effort for monitoring forest bats. Austral Ecology 40:886–897.

Lawrence, B. D., and J. A. Simmons. 1982. Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. The Journal of the Acoustical Society of America 71:585–590.

Lemen, C., P. W. Freeman, J. A. White, and B. R. Andersen. 2015. The Problem of Low Agreement among Automated Identification Programs for Acoustical Surveys of Bats. Western North American Naturalist 75:218–225.

Lenth, R., H. Singmann, J. Love, P. Buerkner, and M. Herve. 2019. R package emmeans: Estimated marginal means.

Limpens, H. J. G. A., and G. F. McCracken. 2002. Choosing a bat detector: theoretical and practical aspects. Pages 28–37 *in* R. M. Brigham, E. K. V. Kalvo, G. Jones, S. Parsons, and H. J. G. A. Limpens, editors. Bat Echolocation Research: Tools, Techniques, and Analysis. Bat Conservation International, Austin, TX.

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 Management 70:1210–1218.

Loeb, S. C., T. J. Rodhouse, L. E. Ellison, C. L. Lausen, J. D. Reichard, K. M. Irvine, T. E. Ingersoll, J. T. H. Coleman, W. E. Thogmartin, J. R. Sauer, C. M. Francis, M. L. Bayless, T. R. Stanley, and D. H. Johnson. 2015. A plan for the North American Bat Monitoring Program (NABat). General Technical Report, U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, NC, USA. <https://www.fs.usda.gov/treesearch/pubs/48442>. Accessed 6 Sep 2019.

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

Lorch, J. M., J. M. Palmer, D. L. Lindner, A. E. Ballmann, K. G. George, K. Griffin, S. Knowles, J. R. Huckabee, K. H. Haman, C. D. Anderson, P. A. Becker, J. B. Buchanan, J. T. Foster, and D. S. Blehert. 2016. First detection of bat white-nose syndrome in Western North America. mSphere 1:e00148-16.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. Andrew Royle, and C. A. Langtimm. 2002. Estimating site occupancy when detection probabilities are less than one. Ecology 83:2248–2255.

McGowan, A. T., and A. S. Hogue. 2016. Bat Occurrence and Habitat Preference on the Delmarva Peninsula. Northeastern Naturalist; Steuben 23:259–276.

Menzel, J. M., W. M. Ford, M. A. Menzel, Timothyc. Carter, J. E. Gardner, J. D. Garner, and J. E. Hofmann. 2005*a*. Summer habitat use and home-range analysis of the endangered Indiana bat. Journal of Wildlife Management 69:430–436.

Menzel, J. M., M. A. Menzel, J. C. Kilgo, W. M. Ford, and J. W. Edwards. 2005*b*. Bat response to Carolina bays and wetland restoration in the southeastern U.S. Coastal Plain. Wetlands 25:542–550.

Michaels, D. 2019. Deadly Bat Fungus Detected in California. CDFW News. <https://cdfgnews.wordpress.com/2019/07/05/deadly-bat-fungus-detected-in-california/>. Accessed 23 Oct 2019.

Millon, L., C. Colin, F. Brescia, and C. Kerbiriou. 2018. Wind turbines impact bat activity, leading to high losses of habitat use in a biodiversity hotspot. Ecological Engineering 112:51–54.

Moore, M. J., D. J. Orth, and E. A. Frimpong. 2017. Occupancy and detection of clinch dace using two gear types. Journal of Fish and Wildlife Management 8:530–543.

Moosman, P. R., J. P. Veilleux, G. W. Pelton, and H. H. Thomas. 2013. Changes in capture rates in a community of bats in New Hampshire during the progression of white-nose syndrome. Northeastern Naturalist 20:552–558.

Murray, K. L., E. R. Britzke, B. M. Hadley, and L. W. Robbins. 1999. Surveying bat communities: a comparison between mist nets and the Anabat II bat detector system. Acta chiropterologica 1:105–112.

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

Muthersbaugh, M. S., W. M. Ford, A. Silvis, and K. E. Powers. 2019*b*. Activity patterns of cave-dwelling bat species during pre-hibernation swarming and post-hibernation emergence in the central Appalachians. Diversity-Basel 11:159.

Niver, R., A. King, M. P. Armstrong, and W. M. Ford. 2014. Methods to evaluate and develop minimum recommended summer survey effort for Indiana bats: White paper. U.S. Fish and Wildlife Service. <https://www.fws.gov/midwest/endangered/mammals/inba/surveys/pdf/WhitePaperIBatSurveyEffort13Jan2014.pdf>. Accessed 27 Feb 2017.

Nocera, Tomás, W. M. Ford, A. Silvis, and C. A. Dobony. 2019. Patterns of acoustical activity of bats prior to and 10 years after WNS on Fort Drum Army Installation, New York. Global Ecology and Conservation 18:e00633.

Nocera, Tomas, W. M. Ford, A. Silvis, and C. A. Dobony. 2019. Let's agree to disagree: comparing auto-acoustic identification programs for Northeastern bats. Journal of Fish and Wildlife Management. <https://www.fwspubs.org/doi/abs/10.3996/102018-JFWM-090>. Accessed 24 Sep 2019.

Norberg, U. M., and J. M. V. Rayner. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London. B, Biological Sciences 316:335–427.

Norquay, K. J. O., F. Martinez-Nuñez, J. E. Dubois, K. M. Monson, and C. K. R. Willis. 2013. Long-distance movements of little brown bats (*Myotis lucifugus*). Journal of Mammalogy 94:506–515.

O'Connor, K. M., L. R. Nathan, M. R. Liberati, M. W. Tingley, J. C. Vokoun, and T. A. G. Rittenhouse. 2017. Camera trap arrays improve detection probability of wildlife: Investigating study design considerations using an empirical dataset. PLoS ONE 12. <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5396891/>. Accessed 3 Apr 2019.

O'Farrell, M. J., and W. L. Gannon. 1999. A comparison of acoustic versus capture techniques for the inventory of bats. Journal of Mammalogy 80:24–30.

O'Keefe, J. M., S. C. Loeb, H. S. Hill Jr., and J. Drew Lanham. 2014. Quantifying clutter: A comparison of four methods and their relationship to bat detection. Forest Ecology and Management 322:1–9.

Omernik, J. M. 1987. Map Supplement: Ecoregions of the Conterminous United States. Annals of the Association of American Geographers 77:118–125.

Otto, C. R. V., and G. J. Roloff. 2011. Using Multiple Methods to Assess Detection Probabilities of Forest-Floor Wildlife. Journal of Wildlife Management 75:423–431.

Owen, S. F., M. A. Menzel, J. W. Edwards, W. M. Ford, J. M. Menzel, B. R. Chapman, P. B. Wood, and K. V. Miller. 2004. Bat activity in harvested and intact forest stands in the Allegheny mountains. Northern Journal of Applied Forestry 21:154–159.

Patriquin, K. J., and R. M. R. Barclay. 2003. Foraging by bats in cleared, thinned and unharvested boreal forest. Journal of Applied Ecology 40:646–657.

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 122:4757.

Pettit, J. L., and J. M. O'Keefe. 2017. Impacts of White-Nose Syndrome Observed During Long-Term Monitoring of a Midwestern Bat Community. Journal of Fish and Wildlife Management 8:69–78.

Powers, K. E., R. J. Reynolds, W. Orndorff, W. M. Ford, and C. S. Hobson. 2015. Post-White-nose syndrome trends in Virginias cave bats, 2008-2013. Journal of Ecology and The Natural Environment 7:113–123.

Pregler, K., J. Vokoun, T. Jensen, and N. Hagstrom. 2015. Using Multimethod Occupancy Estimation Models to Quantify Gear Differences in Detection Probabilities: Is Backpack Electrofishing Missing Occurrences for a Species of Concern? Transactions of the American Fisheries Society 144.

Reichert, B., C. L. Lausen, C. Corben, K. Livengood, J. Szewczak, T. Weller, S. C. Loeb, R. Rodriguez, T. Hohoff, J. Siemers, B. Burkholder, and C. Herzog. 2017. NABat guide to acoustic detectors settings v1.0.

Robbins, L. W., K. L. Murray, and P. M. McKenzie. 2008. Evaluating the effectiveness of the standard mist-netting protocol for the endangered Indiana bat (*Myotis sodalis*). Northeastern Naturalist 15:275–282.

Rockey, C. D., J. P. Stumpf, and A. Kurta. 2013. Additional winter recoveries of Indiana bats (*Myotis sodalis*) banded during summer in Michigan. Northeastern Naturalist 20:N8–N13.

Russo, D., and C. C. Voigt. 2016. The use of automated identification of bat echolocation calls in acoustic monitoring: A cautionary note for a sound analysis. Ecological Indicators 66:598–602.

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

Schirmacher, M. R., S. B. Castleberry, W. M. Ford, and K. V. Miller. 2007. Habitat associations of bats in south-central West Virginia. Proceedings of the Annual Conference of the southeastern association of fish and wildlife agencies. 61: 46-52. 61. <https://www.fs.usda.gov/treesearch/pubs/17269>. Accessed 17 Oct 2019.

Seibold, S., J. Buchner, C. Bässler, and J. Müller. 2013. Ponds in acidic mountains are more important for bats in providing drinking water than insect prey. Journal of Zoology 290:302–308.

Silvis, A., W. M. Ford, E. R. Britzke, N. R. Beane, and J. B. Johnson. 2012. Forest succession and maternity day roost selection by *Myotis septentrionalis* in a mesophytic hardwood forest. International Journal of Forestry Research 2012:e148106.

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 97:1565–1577.

Song Meter SM3BAT bioacoustics recorder user guide. 2018. User Manual, Wildlife Acoustics, Inc., Maynard, MA.

Sparks, D. W., C. M. Ritzi, J. E. Duchamp, and J. O. Whitaker. 2005. Foraging habitat of the Indiana bat (*Myotis sodalis*) at an urban-rural interface. Journal of Mammalogy 86:713–718.

Sprong, L., M. Keith, and E. Seamark. 2012. Assessing the effect of waterproofing on three different bat detectors. African Bat Conservation News 28:4–14.

St. Germain, M. J., A. B. Kniowski, A. Silvis, and W. M. Ford. 2017. Who knew? First *Myotis sodalis* (Indiana Bat) maternity colony in the Coastal Plain of Virginia. Northeastern Naturalist 24:N5–N10.

Starbuck, C. A., S. K. Amelon, and F. R. Thompson. 2015. Relationships between bat occupancy and habitat and landscape structure along a savanna, woodland, forest gradient in the Missouri Ozarks. Wildlife Society Bulletin 31:20–30.

Teets, K. D., S. C. Loeb, and D. S. Jachowski. 2019. Detection probability of bats using active versus passive monitoring. Acta Chiropterologica 21:205–213.

Thogmartin, W. E., R. A. King, P. C. McKann, J. A. Szymanski, and L. Pruitt. 2012. Population-level impact of White-nose Syndrome on the endangered Indiana bat. Journal of Mammalogy 93:1086–1098.

Thogmartin, W. E., C. A. Sanders-Reed, J. A. Szymanski, P. C. McKann, L. Pruitt, R. A. King, M. C. Runge, and R. E. Russell. 2013. White-nose Syndrome is likely to extirpate the endangered Indiana bat over large parts of its range. Biological Conservation 160:162–172.

Timpone, J., K. E. Francl, D. Sparks, V. B. Jr, and J. Beverly. 2011. Bats of the Cumberland Plateau and Ridge and Valley Provinces, Virginia. Southeastern Naturalist 10:515–528.

Tobin, B., and D. Weary. 2004. Digital engineering aspects karst map: a GIS version of Davies, W.E.; Simpson, J.H.; Ohlmacher, G.C.; Kirk, W.S.; and Newton, E.G., 1984, Engineering Aspects of Karst: U.S. Geological Survey, National Atlas of the United States, scale 1:7,500,000. Open-File Report OF-2004-1352, U.S. Geological Survey. <http://pubs.usgs.gov/of/2004/1352/>.

Turner, G., D. Reeder, and J. Coleman. 2011. A Five-year Assessment of Mortality and Geographic Spread of White-Nose Syndrome in North American Bats, with a Look at the Future. Update of White-Nose Syndrome in Bats. Bat Research News 52:13–27.

US Environmental Protection Agency. 2013. Level III Ecoregions of the Conterminous United States. U.S. EPA Office of Research and Development - National Health and Environmental Effects Research Laboratory, Corvallis, OR. <https://www.epa.gov/eco-research/level-iii-and-iv-ecoregions-continental-united-states>.

U.S. Fish and Wildlife Service [USFWS]. 2009. Indiana bat 5-year review: Summary and evaluation. Bloomington Ecological Services Office, Bloomington, Indiana.

<https://www.fws.gov/northeast/nyfo/es/FINAL%20IBat%205-YR%20Review%20093009.pdf>. Accessed 10 Sep 2019.

U.S. Fish and Wildlife Service [USFWS]. 2015. Indiana Bat Range Map and Recovery Units. <https://www.fws.gov/midwest/Endangered/mammals/inba/RangeMapINBA.html>. Accessed 10 Aug 2019.

U.S. Fish and Wildlife Service [USFWS]. 2019*a*. Rangewide Indiana bat summer survey guidance. <http://www.fws.gov/midwest/Endangered/mammals/inba/inbasummersurveyguidance.html>. Accessed 13 Sep 2015.

U.S. Fish and Wildlife Service [USFWS]. 2019*b*. Indiana bat summer survey guidance: Automated acoustic bat id software programs. <https://www.fws.gov/midwest/endangered/mammals/inba/surveys/inbaAcousticSoftware.html>. Accessed 7 Aug 2019.

Virginia Department of Game and Inland Fisheries. 2019. Fish and Wildlife Information Service. <https://vafwis.dgif.virginia.gov/fwis/>. Accessed 30 Oct 2019.

Voigt, C. C., K. Schneeberger, S. L. Voigt-Heucke, and D. Lewanzik. 2011. Rain increases the energy cost of bat flight. Biology Letters 7:793–795.

Waters, D. A., and A. L. Walsh. 1994. The influence of bat detector brand on the quantitative estimation of bat activity. Bioacoustics 5:205–221.

Wei, T., and V. Simko. 2017. R package “corrplot”: Visualization of a Correlation Matrix. <https://CRAN.R-project.org/package=corrplot>. Accessed 18 Aug 2019.

Weller, T. J., and J. A. Baldwin. 2012. Using echolocation monitoring to model bat occupancy and inform mitigations at wind energy facilities. The Journal of Wildlife Management 76:619–631.

Weller, T. J., and C. J. Zabel. 2002. Variation in bat detections due to detector orientation in a forest. Wildlife Society Bulletin 30:922–930.

White-Nose Syndrome Response Team. 2019. White-nose syndrome spread maps. <https://www.whitenosesyndrome.org/static-page/wns-spread-maps>. Accessed 31 Oct 2019.

Wolcott, K. A., and K. Vulinec. 2012. Bat activity at woodland/farmland interfaces in central Delaware. Northeastern Naturalist 19:87–98.

Yates, M. D., and R. M. Muzika. 2006. Effect of forest structure and fragmentation on site occupancy of bat species in Missouri Ozark forests. Journal of Wildlife Management 70:1238–1248.

Table 1: Variables used in candidate models for bat presence from 2,430 site-nights at 30 acoustic sampling sites across Virginia, West Virginia, Ohio, and Kentucky, May - August 2017. See text for complete study site descriptions.

Variable	**Abbreviation**	**Description**	**Type**
Day number	date	Day of the year	Continuous
Precipitation	precip	Binary nightly precipitation	Binary
Basal area	basal	Basal area around detector in m^2/ha	Continuous
Canopy closure	canopy	% of sky covered by overstory vegetation	Continuous
Land cover type	land	Forest-field edge (E), forest corridor (F), or riparian corridor (R)	Categorical
WNS impact-years in 50 km buffer	w50	Mean WNS impact-years in 50 km buffer around study area	Continuous
WNS impact-years in 100 km buffer	w100	Mean WNS impact-years in 100 km buffer around study area	Continuous
WNS impact-years in 150 km buffer	w150	Mean WNS impact-years in 150 km buffer around study area	Continuous
Karst area in 50 km buffer	k50	% of 50 km buffer with karst topography	Continuous
Karst area in 100 km buffer	k100	% of 100 km buffer with karst topography	Continuous
Karst area in 150 km buffer	k150	% of 150 km buffer with karst topography	Continuous
Study site	site	One of the 30 acoustic detector sites	Categorical
Study area	area	One of the 10 study areas	Categorical

Table 2. Total number of call files (calls), recorded and number of nights with presence (Nights) for big brown (*Eptesicus fuscus),* Indiana (*Myotis sodalis*), and northern long-eared (*Myotis septentrionalis*) bats from 2,430 site-nights at 30 acoustic sampling sites across Virginia, West Virginia, Ohio, and Kentucky, May - August 2017. See text for complete study site descriptions.

Study Area	**Sites**	**Sample Nights**	**Big brown**		**Indiana**		**Northern long-eared**	
			Calls	**Nights**	**Calls**	**Nights**	**Calls**	**Nights**
MCB Quantico	3	178	5295	111	NA	NA	129	28
Fort A.P. Hill	3	251	1771	77	465	22	88	0
Canaan NWR	3	273	1224	77	174	45	101	50
Fernow	3	276	6126	127	257	32	26	5
The Jug WMA	3	251	1555	64	195	11	2303	133
Edge of Appalachia	3	209	428	25	70	4	84	13
Fort Knox	3	251	23307	167	92	4	23	2
Riveroak Tract	3	249	719	52	202	15	13	4
Clarks River NWR	3	246	369	16	471	27	149	11
Ballard WMA	3	246	114	9	1852	94	762	75

Table 3. Competing models predicting Indiana bat (*Myotis sodalis*), northern long-eared bat (*Myotis septentrionalis*), and big brown bat (*Eptesicus fuscus)* presence from 2,430 site-nights at 30 acoustic sampling sites across Virginia, West Virginia, Ohio, and Kentucky, May - August 2017. See text for complete variable descriptions.

Model	**K**	**AICc**	**ΔAICc**	ω_i
Indiana bat				
date + date^2 + date^3 + land	8	1260.59	0.00	0.14
date + date^2 + date^3	6	1260.85	0.25	0.12
date + date^2 + date^3 + basal	7	1261.43	0.84	0.09
date + date^2 + date^3 + land + precip	9	1261.93	1.33	0.07
date + date^2 + date^3 + precip	7	1262.18	1.58	0.06
date + date^2 + date^3 + land + basal	9	1262.39	1.80	0.06
date + date^2 + date^3 + land + k150	9	1262.48	1.89	0.05
Northern long-eared bat				
date + land	6	1173.88	0.00	0.14
date + land + w50	7	1173.92	0.04	0.13
date + land + w50 + k50	8	1174.10	0.22	0.12
date + land + basal	7	1174.26	0.38	0.11
date + land + k50	7	1174.66	0.78	0.09
date + land + w50 + basal	8	1174.81	0.93	0.09
date + land + precip	7	1174.95	1.07	0.08
date + land + w50 + precip	8	1175.00	1.12	0.08
date + land + basal + precip	8	1175.33	1.45	0.07
Big brown bat				
date + date^2 + date^3 + land + w150 + k150	10	2228.46	0.00	0.32
date + date^2 + date^3 + land + w150 + k150 + precip	11	2229.29	0.83	0.21
date + date^2 + date^3 + land + w150 + k150 + basal	11	2230.03	1.57	0.15

Table 4. Estimates and 95% confidence intervals (CI) from the best supported two models predicting nightly Indiana bat (*Myotis sodalis*) presence from 2,430 site-nights at 30 acoustic sampling sites across Virginia, West Virginia, Ohio, and Kentucky, May - August 2017. See text for complete variable descriptions.

Model and variables	**Estimate**	**Lower CI**	**Upper CI**
Date only			
(Intercept)	-2.97	-3.75	-2.19
Date	-0.72	-1.08	-0.37
$Date^2$	0.10	-0.06	0.26
$Date^3$	0.25	0.08	0.42
Date and land cover type			
(Intercept)	-3.61	-4.64	-2.59
Date	-0.72	-1.08	-0.36
$Date^2$	0.10	-0.06	0.26
$Date^3$	0.25	0.08	0.42
forested	0.72	-0.42	1.86
riparian	1.30	0.17	2.43

Table 5. Estimates and 95% confidence intervals (CI) from best supported two models predicting nightly northern long-eared bat (*Myotis septentrionalis*) presence from 2,430 site-nights at 30 acoustic sampling sites across Virginia, West Virginia, Ohio, and Kentucky, May- August 2017. See text for complete variable descriptions.

Model and variables	**Estimate**	**Lower CI**	**Upper CI**
Date and land cover			
(Intercept)	-5.55	-7.33	-3.77
date	-0.12	-0.28	0.03
forested	3.28	2.03	4.53
riparian	2.63	1.39	3.87
Date, land cover and WNS			
(Intercept)	-5.55	-7.24	-3.86
date	-0.12	-0.28	0.03
forested	3.28	2.03	4.52
riparian	2.63	1.40	3.86
w50	-0.98	-2.32	0.36

Table 6. Estimates and 95% confidence intervals (CI) from best supported model predicting nightly big brown bat (*Eptesicus fuscus*) presence from 2,430 site-nights at 30 acoustic sampling sites across Virginia, West Virginia, Ohio, and Kentucky, May- August 2017. See text for complete variable descriptions.

Variable	**Estimate**	**Lower CI**	**Upper CI**
(Intercept)	-0.30	-0.97	0.38
date	0.56	0.30	0.81
$date^2$	-0.05	-0.16	0.07
$date^3$	-0.23	-0.35	-0.11
forested	-1.72	-2.56	-0.88
riparian	-0.89	-1.71	-0.06
w150	1.26	0.71	1.80
k150	0.83	0.29	1.37

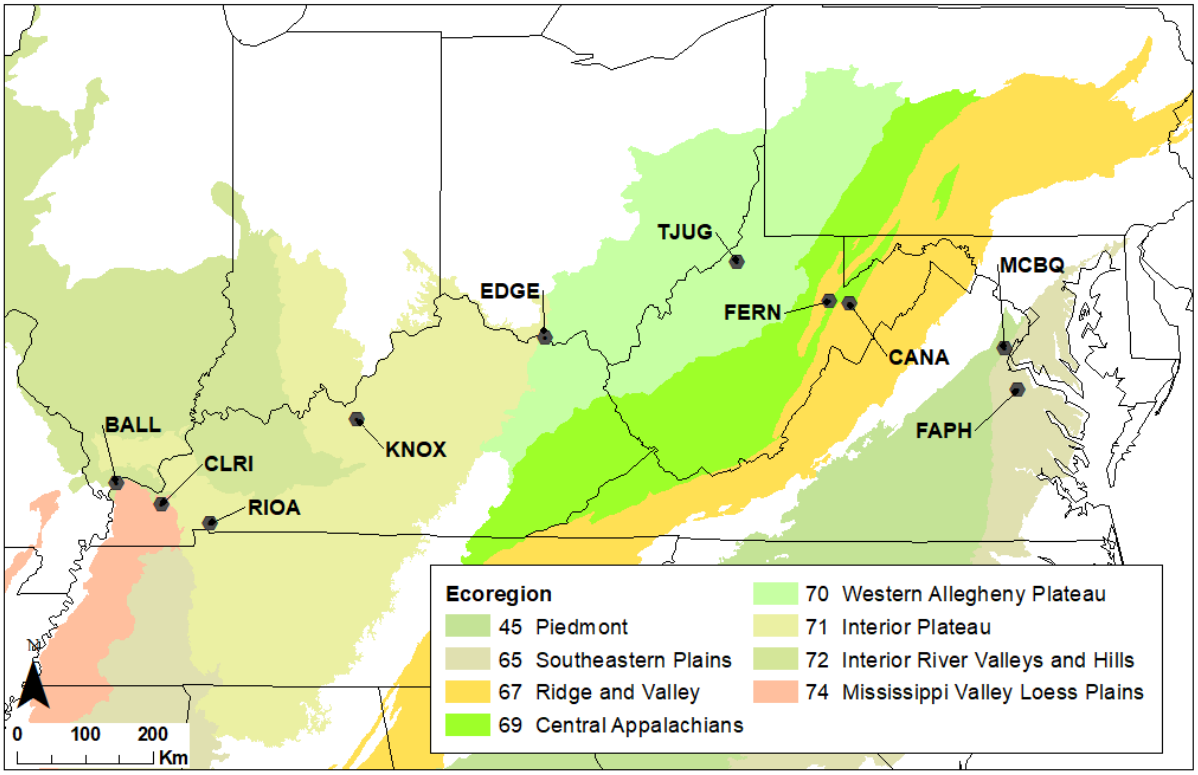

Figure 1. Location of 10 bat acoustic sampling study areas and associated U.S. EPA level III ecoregions, May-August 2017. Study area abbreviations are as follows: BALL, Ballard WMA; CLRI, Clarks River NWR; RIOA, Riveroak Tract; KNOX, Fort Knox; EDGE; Edge of Appalachia Preserve; TJUG, The Jug WMA; FERN, Fernow Experimental Forest; CANA, Canaan Valley NWR; FAPH, Fort A.P. Hill; MCBQ, Marine Corps Base Quantico.

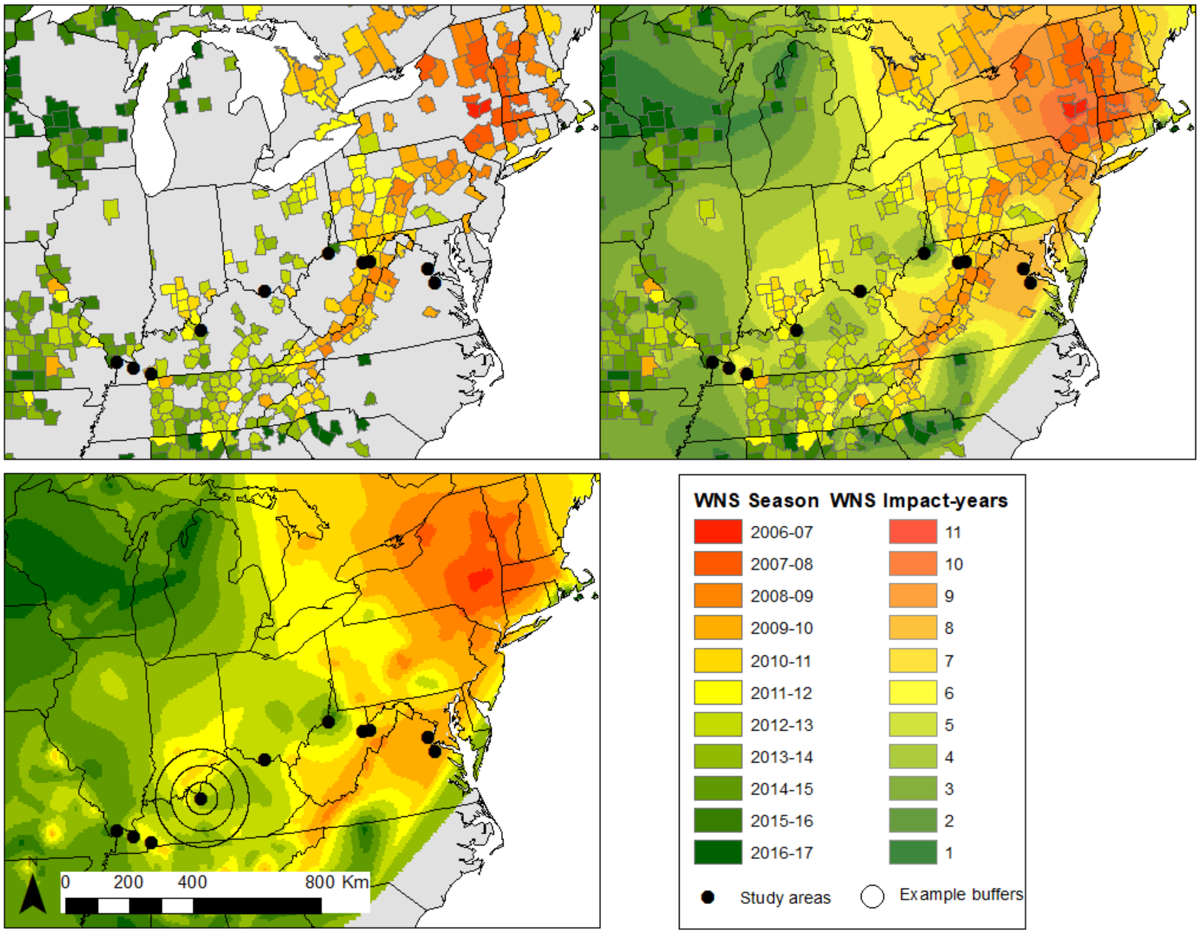

Figure 2. Interpolated white-nose syndrome (WNS) impact-year metric generated using the natural neighbor raster interpolation tool (ESRI, Redlands, CA). County-level WNS detection data accessed from the U.S. Geological Survey, Pennsylvania Game Commission, and https://www.whitenosesyndrome.org. WNS impact-years calculated based on summer 2017 monitoring.

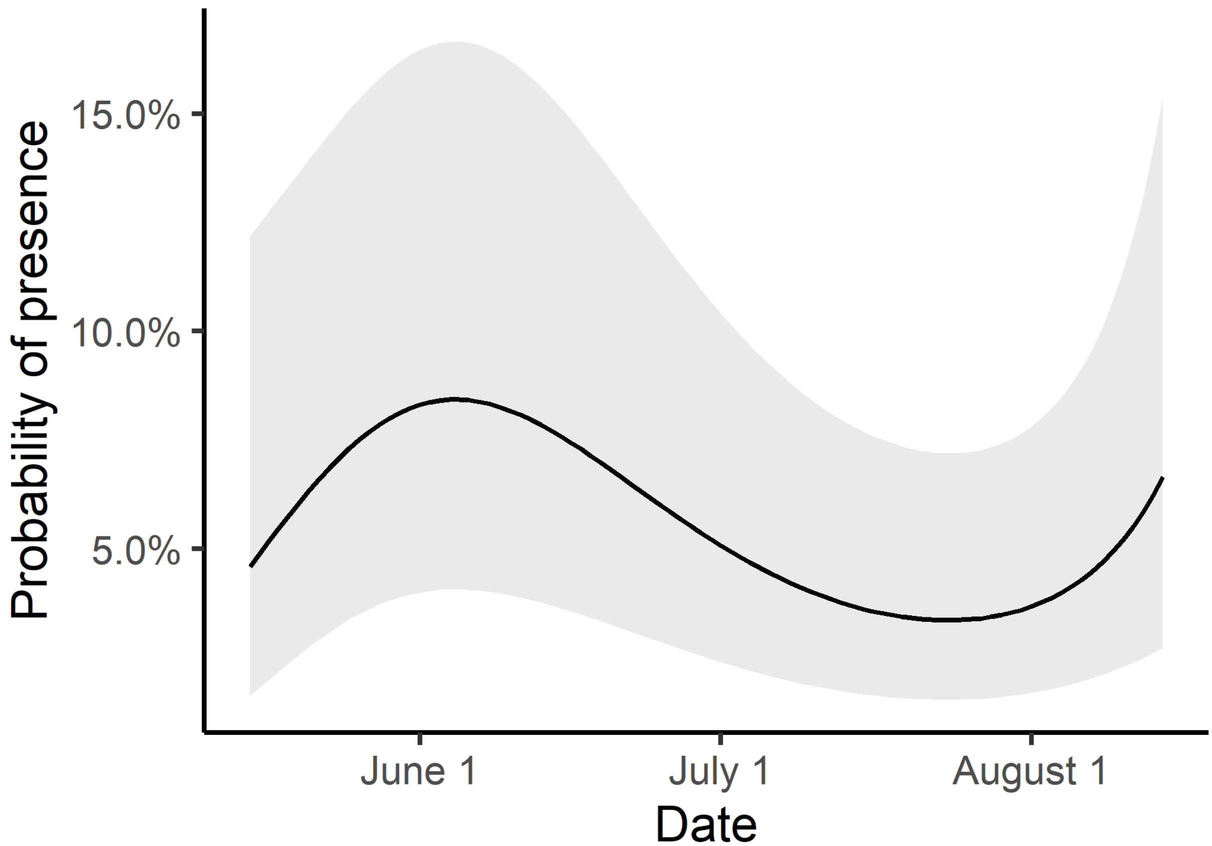

Figure 3. Modeled effect of date on nightly Indiana bat (*Myotis sodalis*) presence with 95% confidence intervals from acoustic sampling with 2,430 site-nights at 30 sites across Virginia, West Virginia, Ohio, and Kentucky, May - August 2017.

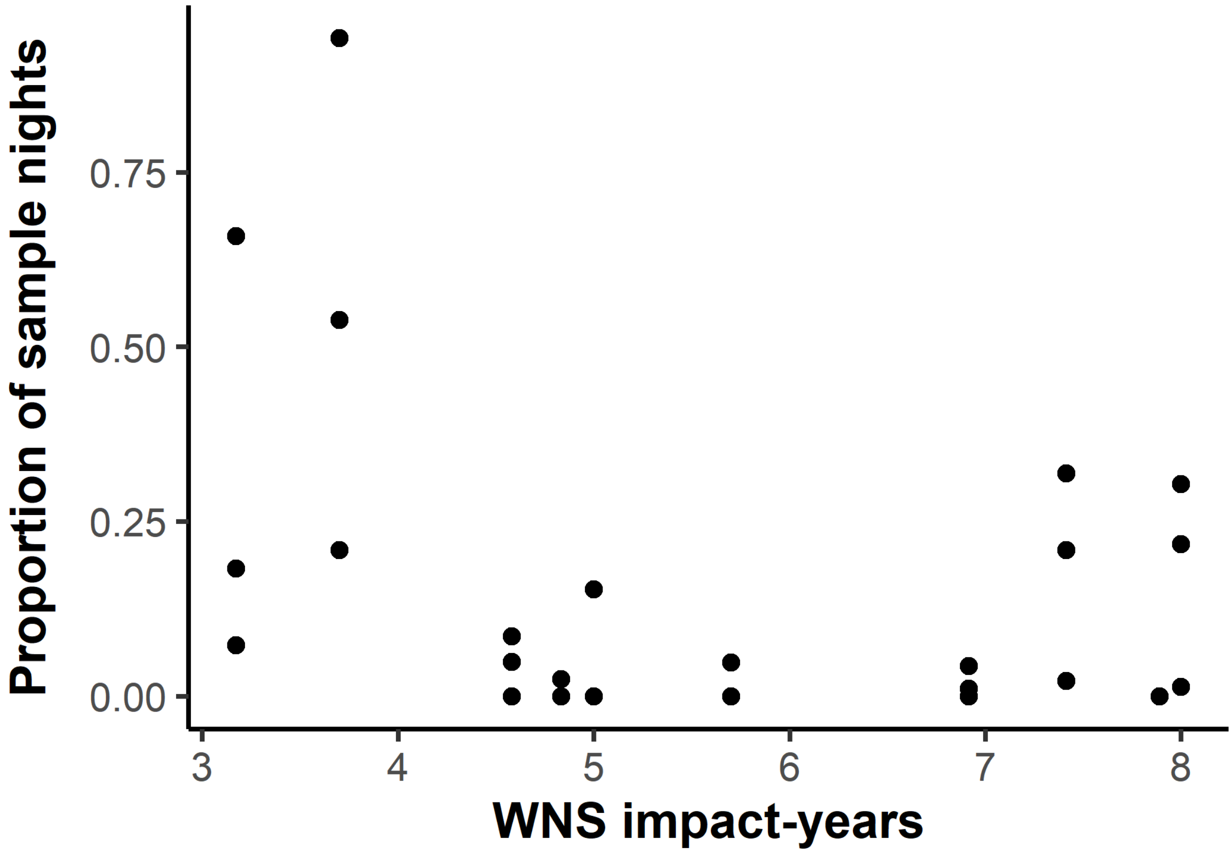

Figure 4. Relationship between the proportion of nights with northern long-eared bat *(Myotis septentrionalis*) presence and number of WNS impact-years from 2,430 site-nights at 30 acoustic sampling sites across Virginia, West Virginia, Ohio, and Kentucky, May - August 2017.

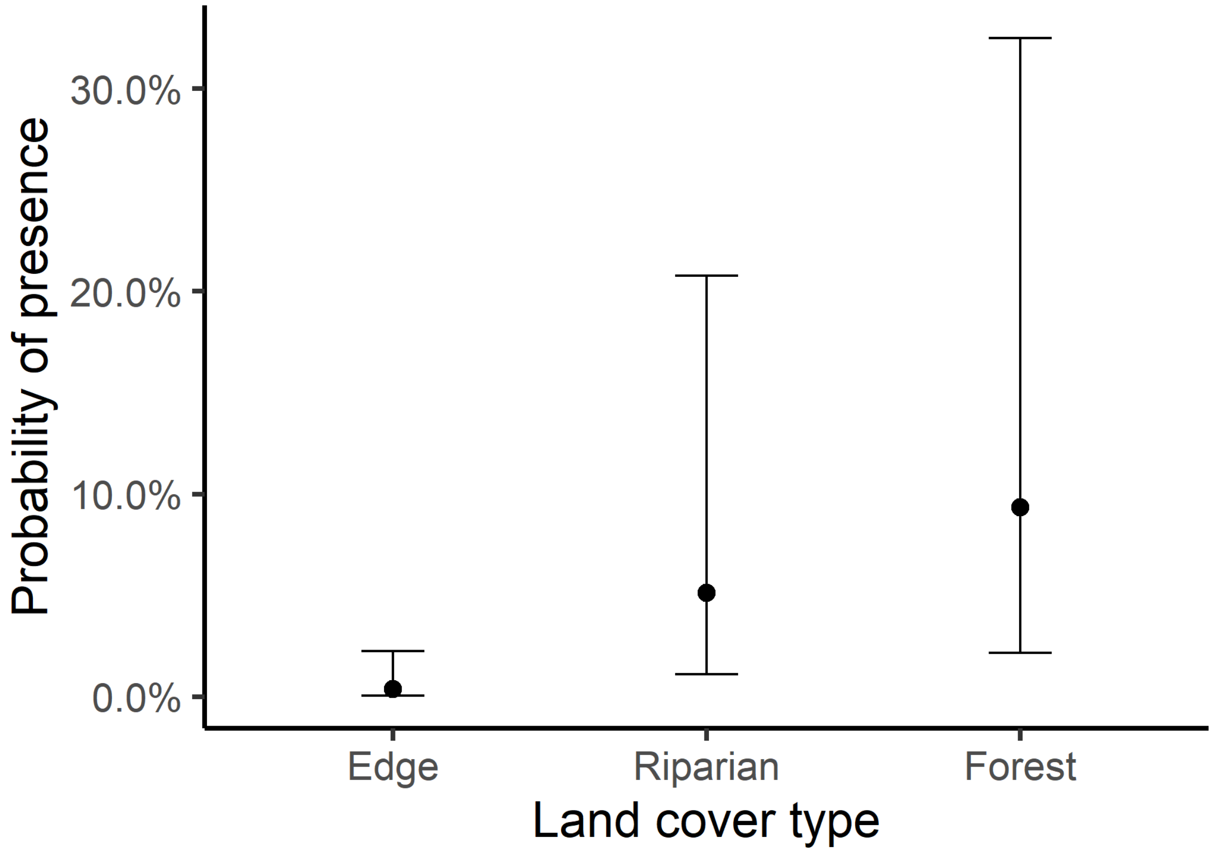

Figure 5. Partial effect plot of land cover type on the predicted probability of nightly northern long-eared bat (*Myotis septentrionalis*) presence with 95% confidence intervals from 2,430 site-nights at 30 acoustic sampling sites across Virginia, West Virginia, Ohio, and Kentucky, May - August 2017.

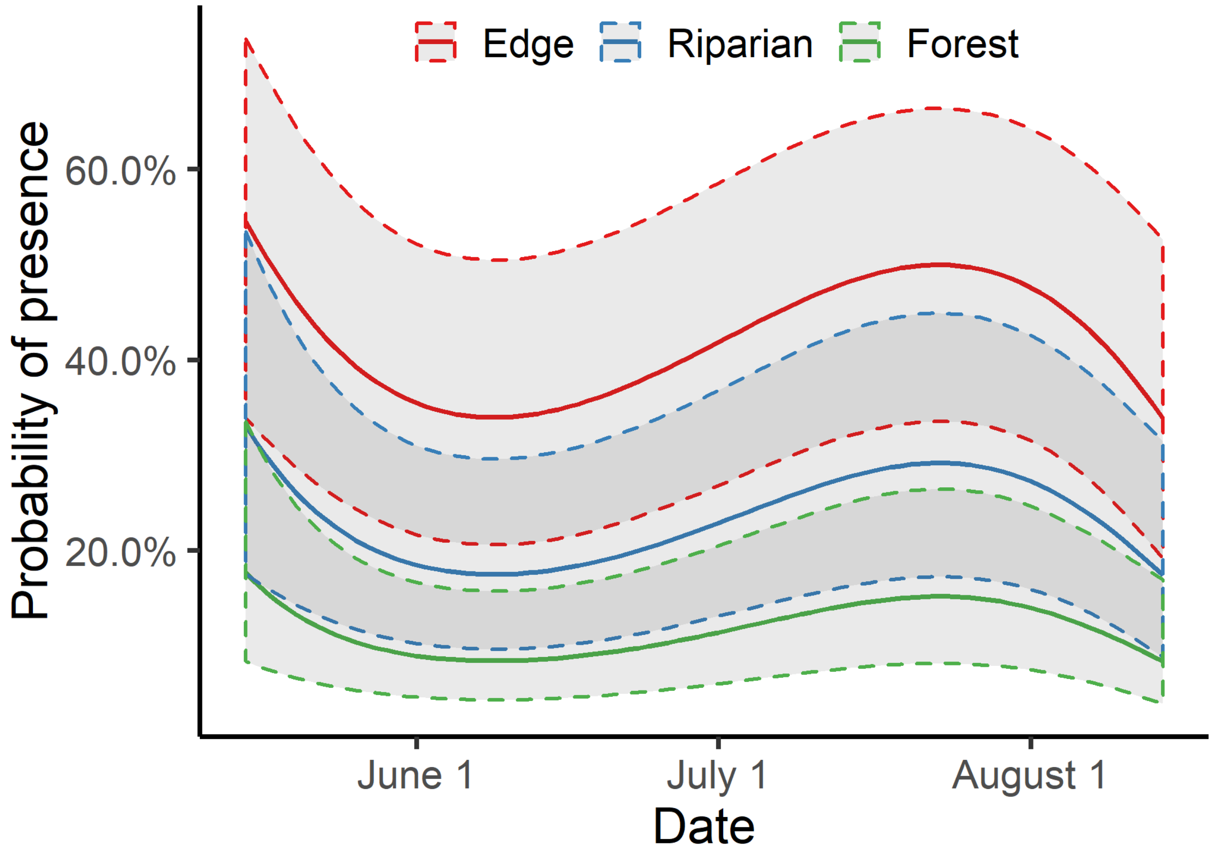

Figure 6. Partial effect plot of date and land cover type on the predicted probability of nightly big brown bat (*Eptesicus fuscus*) presence with 95% confidence intervals from 2,430 site-nights at 30 acoustic sampling sites across Virginia, West Virginia, Ohio, and Kentucky, May - August 2017.

Chapter 2: Bat Acoustic Detector Type Influences Recorded Activity Rates and Detection Probabilities

Abstract

Bat populations across North America currently are threatened by the devastating effects of both White-nose syndrome and wind energy development. Although there are a plethora of available full spectrum and zero-crossing acoustic bat detectors to monitor these declining populations, performance comparisons and the implications to managers thereof are limited. To assess this, I compared five types of acoustic detectors (Pettersson D500X, Anabat Swift, and Wildlife Acoustics SM3BAT in full spectrum and Wildlife Acoustics SM3BAT and Anabat SD2 in zero-crossing) during the summer of 2017 at Fort Knox, Kentucky where the endangered Indiana bat (*Myotis sodalis*), endangered gray bat (*M. griscesens*) and threatened northern long-eared bat (*M. septentrionalis*) occur. I operated all detector types simultaneously at eight sites for 799 detector nights, identified all acoustic data to species or phonic group using Kaleidoscope Pro, and compared all detectors with respect to detection probability and recorded nightly activity. I found that detector type had a significant effect on detection probabilities for all species modeled, however, for common bat species, i.e., eastern red (*Lasiurus borealis*) and big brown (*Eptesicus fuscus*) bats, detectors reached the same 90% detection probability threshold within 2-3 nights of sampling. However, I observed that this level of agreement dropped when comparing detection probability for the more rare Indiana bat. Similarly, I found the highest levels of disagreement for nightly activity of high-frequency bats, whereas mid- and low-frequency bat calls showed moderate levels of disagreement. My findings suggest that each of the detector types tested would suffice for most research and monitoring activities, but standardization of detector type within the scope of a project or study should be encouraged.

Introduction

Bat populations across the United States are currently facing extreme population declines due to the introduction and spread of white-nose syndrome (WNS) and the impacts of wind-energy development. Mist-netting efficiency has declined in WNS-impacted regions, and acoustic detectors use is on the rise (Robbins et al. 2008, Niver et al. 2014). Acoustic monitoring is used for bat surveys investigating research questions such as distributional work, foraging ecology, habitat associations, responses to land management, and the impacts from WNS as well as wind energy development (Johnson et al. 2011, Erickson and West 2003, Austin et al. 2018, Ford et al. 2011, Millon et al. 2018, Menzel et al. 2005*b*). In response to increasing use of acoustic detectors and improved analytical capabilities due to automated analysis and identification software, the U.S. Fish and Wildlife Service (USFWS) has developed acoustic monitoring guidelines to determine presence or absence of two federally listed species: the endangered Indiana bat (*Myotis sodalis*) and the threatened northern long-eared bat (*M. septentrionalis*) using zero-crossing (ZC) or full spectrum (FS) equipment (USFWS 2019*a*). Likewise, the North American Bat Monitoring Program (NABat) provides protocols to acoustically monitor the distribution and abundance of bat populations across the U.S. and Canada with ZC or FS detectors via mobile transect or passive survey approaches (Loeb et al. 2015).

The variety of acoustic detector types available to users has grown concomitant with the increase in acoustic monitoring. For example, NABat provides protocols for using three brands and 11 different models of acoustic detectors (Reichert et al. 2017). Recordings from acoustic detectors may differ due to hardware, i.e., type of microphone, or due to programming or technical differences affecting sensitivity (Waters and Walsh 1994, Fenton et al. 2001, Limpens and McCracken 2002). For example, the ZC detector Anabat SD2 (Titley Scientific, Columbia, MO) detector uses a single setting to determine sensitivity and has options for different frequency division ratios, although using the CFCread program (Titley Scientific, Columbia, MO) users can define the maximum time between calls, smooth parameter, and the minimum line length (Broken-Brow 2018). In contrast, the FS Pettersson D500X (Pettersson Elektronik AB, Uppsala, Sweden), has two options for ultrasonic sampling frequencies, as well as options to set pre-trigger times, recording length, a high pass filter, sampling rate, and trigger sensitivity levels (D500X user's manual 2017).

Regardless of study animal, understanding differences between observation methods is a common need. Often, researchers examine differences in observation methods in terms of variation in detection probability. Defined as the probability of detecting an animal given that it is present in the study area, detection probability is used in occupancy modeling, survival modeling, and abundance estimation to account for imperfect detection (MacKenzie et al. 2002). Studies across taxa, from salamanders, to minnows, to mammals, have demonstrated that different observation methods can result in widely varying detection probabilities, with some differences as great as 80% (Otto and Roloff 2011, Pregler et al. 2015, Moore et al. 2017, O'Connor et al. 2017). Relative to bat monitoring, research has shown that passive acoustic monitoring provides higher detection probabilities than active monitoring in the post-WNS environment (Coleman et al. 2014, Teets et al. 2019) and using two detectors at a study site can improve detection probabilities relative to use of a single detector (Duchamp et al. 2006). In controlled laboratory settings with synthetic ultrasonic calls, detector brands varied in their abilities to record similar numbers of call files based on the distance, angle, and frequency of the sound (Adams et al. 2012, Sprong et al. 2012). Acoustic detectors often record varying numbers and quality of call files of free-flying bats (Waters and Walsh 1994, Adams et al. 2012, Kaiser and O'Keefe 2015). However, even the most recent studies comparing multiple detector types (Adams et al. 2012, Kaiser and O'Keefe 2015) have not included detectors commercially available in the past five years, leaving a critical data gap for managers and researchers.

In addition to detector type effects, bat echolocation frequencies and environmental variables can affect bat detectability and recorded nightly activity. High-frequency echolocation calls attenuate at a higher rate than lower frequency calls as they pass through the atmosphere (Lawrence and Simmons 1982), and accordingly, high-frequency calls are only recorded when bats are relatively close to microphones (Adams et al. 2012). Precipitation can negatively affect echolocation feedback when bats are foraging or navigating through increased attenuation (Griffin 1971) and bats are less likely to switch roosts on nights with increasing rain (Patriquin et al. 2016). These negative impacts and others can result in an overall decrease in bat activity on rainy nights (Erickson and West 2002, Muthersbaugh et al. 2019*a*) or a negative relationship between precipitation and detection probability (Yates and Muzika 2006). Wind speed also can decrease bat presence and lower activity rates due to decreases in foraging efficiency and similar energetic costs to flight (Weller and Baldwin 2012, Muthersbaugh et al. 2019*a*).

Objectives

My objective was to evaluate how acoustic detector type influences bat detection probability and recorded bat nightly activity to inform future monitoring guidelines and provide a resource to examine results across detector types. I additionally examined how nightly wind and precipitation affects both detection probability and recorded nightly activity. I included a variety of older and newer bat acoustic detector models to examine how or if results from past work can be compared to more current work with newer acoustic detector models. I included bat species and phonic groups that covered the spectrum of common eastern U.S. bat species to examine if either detection probability or activity varied by echolocation frequency. I hypothesized that detector type would have a significant impact on both detection probability and recorded bat nightly activity. However, I expected that detectors would reach the same detection probability with cumulative survey nights. I hypothesized that nightly wind and precipitation would have a negative effect on both detection probability and nightly activity. Lastly, I hypothesized that nightly activity of high-frequency bat calls would vary the most among detectors due to attenuation.

Methods

Study Area

I conducted my study at Fort Knox, an U.S. Army military reservation of approximately 44,000 ha located in Meade, Bullitt, and Hardin counties in north-central Kentucky. The Ohio River borders the reservation to the north, with associated midwestern/mid-south bottomland hardwood forest types (Cranfill 1991) and beaver (*Castor canadensis*) ponds. In the upland areas, karst geology with abundant cave resources underlie a western mixed-mesophytic forest type (Dyer 2006). Depending on site quality and past land use, common overstory tree species include white oak (*Quercus alba*), black oak (*Q. velutina*), red oak (*Q. rubra*), shagbark hickory (*Carya ovata*), sugar maple (*Acer saccharum*), yellow poplar (*Liriodendron tulipifera*), white ash (*Fraxinus americana*), and American beech (*Fagus grandifolia*) (Cranfill 1991).

Data Collection

I acoustically surveyed bats at Fort Knox from May 23 - August 16 2017 during the USFWS Indiana bat summer survey sampling period (USFWS 2019*a*). To test for differences among detector types, I operated four different detector models, the Song Meter SM3BAT (SM3BAT) (Wildlife Acoustics Inc., Maynard, MA), Pettersson D500X, AnaBat SD2 (SD2), and AnaBat Swift (Swift) (Titley Scientific, Columbia, MO) in the field at nine different sites. In total, I had five unique detector model/recording style pairs as the Song Meter SM3BAT can record in both FS and ZC file types simultaneously and independently. At each site, I deployed all four detectors simultaneously to record free flying bat echolocation calls for three to four weeks to encompass the eight rain-free nights required in Indiana bat survey protocols (USFWS 2019*a*) and to mimic the longer passive deployments common in more recent studies (Grider et al. 2016, Smith and McWilliams 2016, Muthersbaugh et al. 2019*a*, *b*). I rotated the three detector-comparison groups among sites every three to four weeks resulting in a total of nine sampling locations over the whole summer at Fort Knox. I chose sampling locations based on range accessibility and followed recommended guidelines to ensure sites were suitable for recording high-quality bat calls (i.e., minimal vegetation or other obstructions near the microphone and distant from known day-roosts; Loeb et al. 2015, USFWS 2019*a*).

I based the deployment protocol for each type of detector (Table 7) on methods described in literature and/or manufacturer recommendations (Hourigan and Corben 2012, Loeb et al. 2015, Reichert et al. 2017, D500X user's manual 2017, Song Meter SM3BAT bioacoustics recorder user guide 2018, Broken-Brow 2018). I waterproofed SD2 units using plastic boxes with polyvinyl chloride tubes attached and placed on 1.5 m tripods with a 45^{o} angle (Britzke et al. 2010). I attached all other detector types to trees and placed all omnidirectional, weather-proof microphones away from clutter, elevated on 3.5 m poles, and positioned in the same direction. I deployed omnidirectional microphones within 0.5 m of each other and randomly chose their positions relative to each other at each site. I used eight internal AA batteries to power Swift detectors, and used external power to ensure one month of continued monitoring for all other detectors. At sites with enough solar exposure, I used one 30-watt solar panel (Solartech Power, Inc. Ontario, CA) and three 12 volt, 12 amp-hour batteries to continuously power the

SM3BAT, SD2 and D500x. At sites with limited solar exposure, I used 12 volt, 36 amp-hour batteries to power the three detectors and swapped out recharged batteries between month-long deployments. I programmed detectors to record nightly from 30 minutes before sunset to 30 minutes after sunrise. Because SD2 detectors do not have a variable schedule, I set those to record according to the longest night of the survey period. I used Meteorological Terminal Aviation Routine records from the Fort Knox airport station (https://mesonet.agron.iastate.edu/request/download.phtml) to access hourly weather data. From the downloaded hourly data, I determined average nightly wind speeds and represented nightly precipitation as the proportion of nightly hours with measurable precipitation (Smith and McWilliams 2016).

Data analysis

Following summer recording and compilation of each full site/detector type dataset, I identified bat calls to species using Kaleidoscope version 5.1.0 (Wildlife Acoustics, Maynard, Massachusetts) and classifier 4.2.0 at the "0" setting as recommended by USFWS (USFWS 2019*b*). I used Kaleidoscope because it is the only USFWS approved bat acoustic identification program that can analyze both full spectrum and zero-crossing recordings. When analyzing calls, I included species based on prior documentation through county lists for Kentucky and available data (Silvis et al. 2012, Kentucky Department of Fish and Wildlife 2019). To determine nightly species presence to use in detection probability modeling, I used the threshold set in USFWS Indiana and northern long-eared bat survey guidelines and defined probable presence when identified by the software at a site-night maximum likelihood estimate p-value < 0.05 (USFWS 2019*a*). Because bat acoustic identification programs may incorrectly identify bat species for individual call files (Lemen et al. 2015, Russo and Voigt 2016, Nocera et al. 2019) and to minimize the effects of individual call file misidentification on comparisons among detectors, I also grouped activity data into three species groups: high, medium, and low frequency phonics groups (Kaiser and O'Keefe 2015) for a broader examination of detector comparison. The high frequency group included all *Myotis* species: northern long-eared, Indiana, gray (*M. grisescens*), eastern small-footed (*M. leibii*), and little brown (*M. lucifugus*). The mid-frequency group included eastern red, evening (*Nycticeius humeralis*), and tri-colored bats (*Perimyotis subflavus*). The low frequency group included big brown (*Eptesicus fuscus*), hoary (*Lasiurus cinereus),* and silver-haired bats (*Lasionycteris noctivagans*). I defined nightly activity as the number of call files per species group, per night.

To examine potential differences in detection probability between acoustic detectors, I created single-season, single-species, occupancy models for three commonly detected bat species from different phonic groups. I chose the Indiana bat to represent high frequency calls, the eastern red bat to represent mid-frequency calls, and the big brown bat to represent low frequency calls. Each phonic group represents a different degree of presumed detectability. I limited analysis to sites with detections and assumed species presence (i.e., occupancy = 1) at each site if at least one detector documented presence. I assessed potential correlation among predictors (Table 8) in both detection probability and activity models using R package corrplot (Wei and Simko 2017) to ensure that highly correlated ($r \geq 0.6$) variables were not included in the same model. I centered and scaled all continuous covariates prior to analysis (Schielzeth 2010). I used the SD2 as the reference in both detection probability and recorded nightly activity modeling to enable comparisons between newer acoustic detectors and the older model used in most early passive bat acoustic studies.

I developed seven *a priori* detection probability models for each bat species with weather variables and detector types to address hypotheses about factors that might impact acoustic detection probabilities. I treated each site-detector type combination as a unique detection history, treated detector type as a site-level covariate and nightly weather as an observation level covariate. I built models in package unmarked (Fiske and Chandler 2011) in program R version 3.6.0 (R Core Team 2019) and used an information theoretic approach to compare models, with Akaike's Information Criterion (AIC) corrected for small sample size and considered those competing models with a ΔAICc < 2 (Burnham and Anderson 2002). When developing the USFWS Indiana bat survey design, researchers examined the level of survey effort needed to reach 90% confidence in any negative result (Niver et al. 2014). I used detection probabilities predicted from best supported models for each species to generate cumulative detection curves (Moore et al. 2017) and determined how many sample nights each detector type needed to reach the 90% detection probability threshold.

To examine potential differences in recorded nightly bat activity between acoustic detectors, I developed a set of *a priori* models including weather variables, day of the year, and detector type to represent hypotheses about what might influence phonic-group recordings. After testing for overdispersion, I modeled nightly activity separately for each phonic group using negative binomial generalized linear mixed models (GLMMs) in program R version 3.6.0 (R Core Team 2019) with package glmmTMB (Brooks et al. 2017) with a random effect of site. I used an information theoretic approach to compare models, with Akaike's Information Criterion (AIC) corrected for small sample size (AICc from package bbmle, Bolker 2017; Burnham and Anderson 2002) and considered those best supported models with a ΔAICc < 2. If detector type was significant in best supported models, I conducted *post-hoc* pairwise comparisons of estimated marginal means using a Tukey's test adjusted for multiple comparisons with R package emmeans (Lenth et al. 2019).

Results

During the summer of 2017, I sample nine sites, but removed one because of high volumes of insect and other extraneous ultrasonic noise, leaving eight sites with 799 detector site-nights (Table 9). Detector failures and full SD cards led to uneven sampling periods for detectors. Kaleidoscope identified 82,625 call files to species across all recording types. I documented big brown and eastern red bat presence at all eight sites. I detected Indiana bats at five out of the eight sites at Fort Knox, and restricted my detection probability analysis to those five sites to avoid introducing a negative bias in the data.

Detection probability

Although there were multiple competing models within ΔAICc < 2 for both Indiana and eastern red bats, detector type alone was the most parsimonious model (Table 10). Additionally, for Indiana and eastern red bats, detection models including only weather variables were no better than the null model. For Indiana bats, all detector types had significantly higher detection probabilities than the SD2 (Table 11). Only the SM3BAT in FS had significant higher detection probabilities of eastern red bats relative to the SD2 (Table 12). In contrast, wind, precipitation, and detector type were significant factors influencing big brown bat detection probability; both wind and precipitation had negative associations with small effect sizes. All detector types had significantly higher big brown bat detection probabilities compared to the SD2 (Table 13). The differences in cumulative detection probabilities among detector types were greatest for the Indiana bat; the number of survey nights needed to reach a 90% detection probability threshold ranged from two to 15 (Figure 7). Detection probabilities for the eastern red bat varied the least; all detectors reached a 90% threshold in two to three nights (Figure 8). Although the SD2 had a lower big brown bat detection probability relative to the other four detector types, the difference was not as large compared to the Indiana bat results and all detectors reached 90% detection probability within four nights (Figure 9).

Call file comparison

Detector type was a significant factor in predicting nightly recorded bat activity for all three phonic groups. For high-frequency bats, the best supported model included detector type, average nightly wind speed and day of the year (Table 14). All three variables were significant, and both date and wind had positive relationships with nightly activity, although the effect size for wind was small (Table 15). The SM3BAT in FS recorded significantly higher nightly activity compared to the SD2, whereas the other three detector styles recorded significantly lower nightly activity. *Post-hoc* pairwise comparisons showed that the Swift did not record significantly different high-frequency bat activity levels from the SM3BAT in ZC, but that all other pairwise comparisons were significantly different (Figure 10).

For mid-frequency bats, there were five competing models, although the detector type and wind model was the most parsimonious of the competing models (Table 14). Detector type and wind were the only significant variables and wind had a significant positive relationship with nightly activity, although again the effect size was small (Table 16). The SM3BAT in both FS and ZC recorded significantly more calls than the SD2, but the D500X and Swift showed no significant difference from the SD2 reference. *Post-hoc* pairwise comparisons showed the SM3BAT in FS recorded significantly higher activity levels from all other detectors and the SM3BAT in ZC recorded significantly higher activity levels than the SD2, but all other comparisons were not significantly different (Figure 10).

There were three competing models predicting low-frequency bat activity, and detector type alone was the most parsimonious competing model (Table 14). Although both date and wind were in competing models, neither variable had a significant effect on low-frequency bat activity (Table 17). There was no significant difference in nightly activity between the SM3BAT in FS and the SD2, but the SM3BAT in ZC, the D500X and the Swift all recorded significantly fewer low-frequency nightly call files than the SD2. *Post-hoc* pairwise comparisons showed that the SM3BAT in FS recorded significantly higher activity levels from all other detectors except the SD2, and the SD2 recorded significantly higher activity levels than the Swift and D500x, but all other comparisons were not significantly different (Figure 10).

Discussion

This study allowed me to compare a novel range of newer and older bat detector models in the field with both FS and ZC recording styles and examine how they performed with respect to detection probability and recorded nightly activity. Consistent with my expectations, detector type significantly influenced both detection probability and recorded nightly bat activity for all species and phonic groups. Although I found differences in the number of nights acoustic detectors needed to reach a 90% detection probability threshold, taken as a group, there were more similarities than differences. For example, the SM3BAT ZC and the Swift FS were consistently similar in both nightly call file numbers and detection probability, despite different manufacturers and recording styles. However, I found the greatest differences among detectors when examining high-frequency recorded bat activity and detection probability for Indiana bats.

Although all four detector types varied in detection probability relative to the SD2, with multiple sampling nights the discrepancies lessened. For the relatively common eastern red and big brown bats, all detector types reached the 90% detection probability threshold within two or three nights. However, with the more rare Indiana bat, there was greater variability in the duration of nights detectors needed to reach the 90% detection probability threshold. This result aligned with my hypothesis that after multiple sample nights, detectors would reach the same detection probability. O’Connor et al. (2017) found similar results in that camera arrays varying from 2-10 detectors reached the same threshold after multiple survey nights, although the number of surveys needed to reach the same detection probability varied by the detectability of the animal surveyed, with harder to detect Virginia opossums (*Didelphis virginiana*) needing more survey nights than white-tailed deer (*Odocoileus virginianus*). Similarly, Moore et al. (2017) found that although electrofishing had higher detection probabilities than minnow traps, the two methods reached the same 95% detection probability after six survey attempts.

Consistent with my expectations, the high-frequency phonic group showed the greatest difference in pairwise comparisons of recorded activity between detectors. High-frequency sounds attenuate through the atmosphere (Lawrence and Simmons 1982) and the greatest differences between detectors are often tied to high- frequency calls (Adams et al. 2012, Kaiser and O'Keefe 2015). However, these differences could be due to even minor differences in microphone placement: Weller and Zabel (2002) found that relatively small variance in microphone positioning led to significant differences in recorded bat activity and call quality at the same survey site. Although recorded nightly activity from mid- and low-frequency phonic groups showed more agreement, there were still significant differences. Such differences for monitoring low-frequency bats might be a concern to managers, as species such as the hoary bat are most impacted by wind energy and therefore are a highlighted species to monitor (Arnett and Baerwald 2013). Echolocation activity often is used to provide a more nuanced insight into bat associations than presence-absence studies, including examining responses to land management, disturbance, or weather associations (Menzel et al. 2005*b*, Johnson et al. 2008, Austin et al. 2018, Muthersbaugh et al. 2019*a*). Habitat, habitat and/or specific species use distinctions could be lost if multiple detector types are used in a study due to differences in detector recording capabilities, thereby producing biased or erroneous conclusions.

Unexpectedly, nightly precipitation and wind had a statistically significant negative effect only on detection probability of big brown bats. In all other models, weather variables had either no significant effect or a small positive effect on both detection probability and nightly activity. However, average nightly wind speeds recorded at Fort Knox rarely exceeded the 10 mph threshold that may be indicative of when wind has a negative impact on activity (Arnett et al. 2011). Similarly, very few nights during my survey had precipitation recorded for more than 80% of the night hours and most nights recorded with rain had less than 35% of the night hours. Light rain has less effect on bat foraging activity (Erkert 1982), and other studies examining detection probability found no significant effect of precipitation (Austin et al. 2019, Teets et al. 2019). Thus, weather may only be a concern in bat acoustic monitoring when wind or rain surpass biologically or acoustically relevant thresholds.

Survey implications

Although there was significant variation among detectors with respect to recorded nightly activity, all five detector types reached the same 90% detection probability threshold within five nights for all three species analyzed, with the exception of the SD2 for Indiana bats. My results indicate that most detectors would be adequate for use in USFWS presence/absence surveys for Indiana and potentially for northern long-eared bats (USFWS 2019*a*). However, the low SD2 Indiana bat detection probability is of concern for monitoring efforts going forward and warrants further examination in that historic data collected with this equipment may be biased towards false negative findings.

Regardless of detector type, no detector inerrantly records all bat echolocation calls within its putative sampling cone. Adams et al. (2012) found that even the best-performing detector only recorded 25% of calls in a lab-based playback experiment. When comparing results from two of same model of detector deployed 10m apart in the field, Kubista and Bruckner

(2017) observed differences in in bat species richness and activity. Even when using the same detector type, surveyors need to sample multiple sites (Deeley 2019) and across multiple nights (Law et al. 2015). Weather variables may be important to take into account when conducting short acoustic deployments or surveying to determine presence or absence of a federally listed species (Loeb et al. 2015, USFWS 2019*a*), however my results show that multi-week or month surveys may not need the same level of concern.

Literature Cited

Adams, A. M., M. K. Jantzen, R. M. Hamilton, and M. B. Fenton. 2012. Do you hear what I hear? Implications of detector selection for acoustic monitoring of bats. Methods in Ecology and Evolution 3:992–998.

Agranat, I. 2014. Detecting bats with ultrasonic microphones: Understanding the effects of microphone variance and placement on detection rates. Wildlife Acoustics, Inc., Maynard, MA.

Aldridge, H. D. J. N., and I. L. Rautenbach. 1987. Morphology, echolocation and resource partitioning in insectivorous bats. Journal of Animal Ecology 56:763–778.

Altringham, J. D. 2011. Bats: From Evolution to Conservation. OUP Oxford.

Arnett, E. B., and E. F. Baerwald. 2013. Impacts of wind energy development on bats: implications for conservation. Pages 435–456 *in* R. A. Adams and S. C. Pedersen, editors. Bat Evolution, Ecology, and Conservation. Springer New York.

Arnett, E. B., M. M. Huso, M. R. Schirmacher, and J. P. Hayes. 2011. Altering turbine speed reduces bat mortality at wind-energy facilities. Frontiers in Ecology and the Environment 9:209–214.

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 38:183–195.

Austin, L. V., A. Silvis, W. Mark Ford, and K. E. Powers. 2019. Effects of historic wildfire and prescribed fire on site occupancy of bats in Shenandoah National Park, Virginia, USA. Journal of Forestry Research 1–16.

Bender, M. J., S. B. Castleberry, D. A. Miller, and T. Bently Wigley. 2015. Site occupancy of foraging bats on landscapes of managed pine forest. Forest Ecology and Management 336:1–10.

Blakey, R. V., E. B. Webb, D. C. Kesler, R. B. Siegel, D. Corcoran, and M. Johnson. 2019. Bats in a changing landscape: Linking occupancy and traits of a diverse montane bat community to fire regime. Ecology and Evolution 9:5324–5337.

Bolker, B. 2017. Tools for General Maximum Likelihood Estimation. <https://cran.r-project.org/web/packages/bbmle/bbmle.pdf>. Accessed 10 Aug 2019.

Britzke, E. R., A. C. Hicks, S. L. Von Oettingen, and S. R. Darling. 2006. Description of spring roost trees used by female Indiana bats (*Myotis sodalis*) in the Lake Champlain Valley of Vermont and New York. The American Midland Naturalist 155:181–187.

Britzke, E. R., B. A. Slack, M. P. Armstrong, and S. C. Loeb. 2010. Effects of orientation and weatherproofing on the detection of bat echolocation calls. Journal of Fish and Wildlife Management 1:136–141.

Broken-Brow, J. 2018. AnaBat Swift bat detector user manual. User Manual, Titley Scientific, Columbia, Missouri, USA.

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker. 2017. Modeling zero-inflated count data with glmmTMB. bioRxiv 132753.

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

Brooks, R. T., and W. M. Ford. 2005. Bat activity in a forest landscape of central Massachusetts. Northeastern Naturalist 12:447–462.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Springer, New York, NY.

Childs, C. 2004. Interpolating Surfaces in ArcGIS Spatial Analyst. ArcUser July-September:32–35.

Christman, M. C., D. H. Doctor, M. L. Niemiller, D. J. Weary, J. A. Young, K. S. Zigler, and D. C. Culver. 2016. Predicting the occurrence of cave-inhabiting fauna based on features of the earth surface environment. PLOS ONE 11:e0160408.

Coleman, J. 2014. White-Nose Syndrome The devastating disease of hibernating bats in North America. US Fish & Wildlife Publications. <https://digitalcommons.unl.edu/usfwspubs/453>.

Coleman, L. S., W. M. Ford, C. A. Dobony, and E. R. Britzke. 2014. A comparison of passive and active acoustic sampling for a bat community impacted by White-nose Syndrome. Journal of Fish and Wildlife Management 5:217–226.

Cox, M. R., E. V. Willcox, P. D. Keyser, and A. L. Vander Yacht. 2016. Bat response to prescribed fire and overstory thinning in hardwood forest on the Cumberland Plateau, Tennessee. Forest Ecology and Management 359:221–231.

Cranfill, R. 1991. Flora of Hardin County, Kentucky. Castanea 56:228–267.

D500X user’s manual. 2017. User Manual, Pettersson Elektronik AB, Uppsala, Sweden.

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

De La Cruz, J., R. L. Ward, and E. S. Schroder. 2018. Landscape characteristics related to use of artificial roosts by northern long-eared bats in north-central West Virginia. Northeastern Naturalist 25:487–501.

Deeley, S. 2019. Ecology of mid-Atlantic bats post-WNS: Communities, diet, and reproduction along an urban-to-rural gradient. Dissertation, Virginia Polytechnic Institute and State University, Blacksburg, VA, USA.

Dowling, Z. R., and D. I. O'Dell. 2018. Bat use of an island off the coast of Massachusetts. Northeastern Naturalist 362–382.

Duchamp, J. E., M. Yates, R.-M. Muzika, and R. K. Swihart. 2006. Estimating probabilities of detection for bat echolocation calls: an application of the double-observer method. Wildlife Society Bulletin 34:408–412.

Dyer, J. M. 2006. Revisiting the deciduous forests of eastern North America. BioScience 56:341–352.

Dzal, Y., L. P. McGuire, N. Veselka, and M. B. Fenton. 2011. Going, going, gone: the impact of white-nose syndrome on the summer activity of the little brown bat (*Myotis lucifugus*). Biology Letters 7:392–394.

Erickson, J. L., and S. D. West. 2002. The influence of regional climate and nightly weather conditions on activity patterns of insectivorous bats. Acta Chiropterologica 4:17–24.

Erickson, J. L., and S. D. West. 2003. Associations of bats with local structure and landscape features of forested stands in western Oregon and Washington. Biological Conservation 109:95–102.

Erkert, H. G. 1982. Ecological Aspects of Bat Activity Rhythms. Pages 201–242 *in* T. H. Kunz, editor. Ecology of Bats. Springer US, Boston, MA.

Fenton, M. B., S. Bouchard, M. J. Vonhof, and J. Zigouris. 2001. Time-expansion and zero-crossing period meter systems present significantly different views of echolocation calls of bats. Journal of Mammalogy 82:721–727.

Fiske, I., and R. Chandler. 2011. unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Ford, D., and P. Williams. 2013. Introduction to Karst. Pages 1–8 *in*. Karst Hydrogeology and Geomorphology. John Wiley & Sons, Ltd.

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 2:125–134.

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 126:528–539.

Francl, K. E., W. M. Ford, D. W. Sparks, and V. Brack. 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 3:33–42.

Frank, C. L., A. Michalski, A. A. McDonough, M. Rahimian, R. J. Rudd, and C. Herzog. 2014. The resistance of a North American bat species (*Eptesicus fuscus*) to white-nose syndrome (WNS). PLoS ONE 9:e113958.

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 329:679–682.

Frick, W. F., S. J. Puechmaille, J. R. Hoyt, B. A. Nickel, K. E. Langwig, J. T. Foster, K. E. Barlow, T. Bartonička, D. Feller, A.-J. Haarsma, C. Herzog, I. Horáček, J. van der Kooij, B. Mulkens, B. Petrov, R. Reynolds, L. Rodrigues, C. W. Stihler, G. G. Turner, and A.

M. Kilpatrick. 2015. Disease alters macroecological patterns of North American bats. Global Ecology and Biogeography 24:741–749.

Fukui, D., M. Murakami, S. Nakano, and T. Aoi. 2006. Effect of emergent aquatic insects on bat foraging in a riparian forest. Journal of Animal Ecology 75:1252–1258.

Furey, N. M., and P. A. Racey. 2016. Conservation Ecology of Cave Bats. Pages 463–500 *in* C. C. Voigt and T. Kingston, editors. Bats in the Anthropocene: Conservation of Bats in a Changing World. Springer International Publishing, Cham.

Geipel, I., M. J. Smeekes, W. Halfwerk, and R. A. Page. 2019. Noise as an informational cue for decision-making: the sound of rain delays bat emergence. Journal of Experimental Biology 222:jeb192005.

Grider, J. F., A. L. Larsen, J. A. Homyack, and M. C. Kalcounis-Rueppell. 2016. Winter activity of coastal plain populations of bat species affected by white-nose syndrome and wind energy facilities. PLoS One 11:e0166512.

Griffin, D. R. 1971. The importance of atmospheric attenuation for the echolocation of bats (Chiroptera). Animal Behaviour 19:55–61.

Grindal, S. D., J. L. Morissette, and R. M. Brigham. 1999. Concentration of bat activity in riparian habitats over an elevational gradient. Canadian Journal of Zoology 77:972–977.

Hauer, C., L. Powers, D. Mcnaughton, C. Paul, and B. Sewall. 2019. Changes in a summer bat community in southeastern Pennsylvania. Journal of the Pennsylvania Academy of Science 93:47–62.

Hawkins, J. A., M. K. Gooden, G. G. Janos, and P. L. Sewell. 2017. Fall 2016/Winter 2017 NCDOT Northern Long-eared Bat Research Project, Bertie, Bladen, Hyde, Martin, and

Tyrrell Counties, North Carolina. Copperhead Environmental Consulting, INC., Paint Lick, Kentucky.

Hein, C. D., S. B. Castleberry, and K. V. Miller. 2009. Site-occupancy of bats in relation to forested corridors. Forest Ecology and Management 257:1200–1207.

Holliday, C. 2012. 2012 White-nose Syndrome disease surveillance and bat population monitoring report: A report of the Tennessee WNS Response Cooperators. Tennessee Chapter of The Nature Conservancy. <http://www.tnbwg.org/2012%20White%20Nose%20Syndrome%20Report.pdf>. Accessed 2 Oct 2019.

Hourigan, C., and C. Corben. 2012. AnaBat SD2 compact flash detector user manual. User Manual, Titley Scientific, Columbia, Missouri, USA.

Huebschman, J. J. 2019. Bats in southwest Wisconsin during the era of white-nose syndrome. Northeastern Naturalist 26:168–182.

Humes, M. L., J. P. Hayes, and M. W. Collopy. 1999. Bat activity in thinned, unthinned, and old-growth forests in western Oregon. The Journal of Wildlife Management 63:553–561.

Hyzy, B. A., R. E. Russell, A. Silvis, W. M. Ford, J. Riddle, and K. Russel. In press. Investigating maternity roost selection of northern long-eared bats at three sites in Wisconsin. Endangered Species Research.

Ingersoll, T. E., B. J. Sewall, and S. K. Amelon. 2013. Improved analysis of long-term monitoring data demonstrates marked regional declines of bat populations in the eastern United States. PLoS ONE 8:e65907.

Ingersoll, T. E., B. J. Sewall, and S. K. Amelon. 2016. Effects of white-nose syndrome on regional population patterns of 3 hibernating bat species. Conservation Biology 30:1048–1059.

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

Jachowski, D. S., J. B. Johnson, C. A. Dobony, J. W. Edwards, and W. M. Ford. 2014*b*. Space use and resource selection by foraging Indiana bats at the northern edge of their distribution. Endangered Species Research 24:149–157.

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

Johnson, J. B., J. W. Edwards, and W. M. Ford. 2011. Nocturnal activity patterns of northern myotis (*Myotis septentrionalis*) during the maternity season in West Virginia (USA). Acta Chiropterologica 13:391–397.

Johnson, J. B., W. M. Ford, J. W. Edwards, and M. A. Menzel. 2010. Bat community structure within riparian areas of northwestern Georgia, USA. Folia Zoologica 59:192–202.

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.

Kaiser, Z. D. E., and J. M. O’Keefe. 2015. Data acquisition varies by bat phonic group for 2 types of bat detectors when weatherproofed and paired in field settings. Wildlife Society Bulletin 39:635–644.

Kentucky Department of Fish and Wildlife. 2019. Bats of Kentucky. <https://fw.ky.gov/Wildlife/Pages/Bats-of-Kentucky.aspx>. Accessed 30 Oct 2019.

Krauel, J. J., L. P. McGuire, and J. G. Boyles. 2017. Testing traditional assumptions about regional migration in bats. Mammal Research 1–9.

Kubista, C., and A. Bruckner. 2017. Within-Site Variability of Field Recordings from Stationary, Passively Working Detectors. Acta Chiropterologica 19:189–197.

Kurta, A., and S. W. Murray. 2002. Philopatry and migration of banded Indiana bats (*Myotis sodalis*) and effects of radio transmitters. Journal of Mammalogy 83:585–589.

Kurta, A., S. W. Murray, and D. H. Miller. 2002. Roost selection and movements across the summer landscape. Pages 118–129 *in* A. Kurta and J. Kennedy, editors. The Indiana bat: biology and management of an endangered species. Bat Conservation International, Austin, Texas, USA.

Lacki, M. J., J. P. Hayes, and A. Kurta. 2007. Bats in forests: Conservation and management. JHU Press.

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

Law, B., L. Gonsalves, P. Tap, T. Penman, and M. Chidel. 2015. Optimizing ultrasonic sampling effort for monitoring forest bats. Austral Ecology 40:886–897.

Lawrence, B. D., and J. A. Simmons. 1982. Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. The Journal of the Acoustical Society of America 71:585–590.

Lemen, C., P. W. Freeman, J. A. White, and B. R. Andersen. 2015. The Problem of Low Agreement among Automated Identification Programs for Acoustical Surveys of Bats. Western North American Naturalist 75:218–225.

Lenth, R., H. Singmann, J. Love, P. Buerkner, and M. Herve. 2019. R package emmeans: Estimated marginal means.

Limpens, H. J. G. A., and G. F. McCracken. 2002. Choosing a bat detector: theoretical and practical aspects. Pages 28–37 *in* R. M. Brigham, E. K. V. Kalvo, G. Jones, S. Parsons, and H. J. G. A. Limpens, editors. Bat Echolocation Research: Tools, Techniques, and Analysis. Bat Conservation International, Austin, TX.

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 Management 70:1210–1218.

Loeb, S. C., T. J. Rodhouse, L. E. Ellison, C. L. Lausen, J. D. Reichard, K. M. Irvine, T. E. Ingersoll, J. T. H. Coleman, W. E. Thogmartin, J. R. Sauer, C. M. Francis, M. L. Bayless, T. R. Stanley, and D. H. Johnson. 2015. A plan for the North American Bat Monitoring Program (NABat). General Technical Report, U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, NC, USA.

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

Lorch, J. M., J. M. Palmer, D. L. Lindner, A. E. Ballmann, K. G. George, K. Griffin, S. Knowles, J. R. Huckabee, K. H. Haman, C. D. Anderson, P. A. Becker, J. B. Buchanan, J. T.

Foster, and D. S. Blehert. 2016. First detection of bat white-nose syndrome in Western North America. mSphere 1:e00148-16.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. Andrew Royle, and C. A. Langtimm. 2002. Estimating site occupancy when detection probabilities are less than one. Ecology 83:2248–2255.

McGowan, A. T., and A. S. Hogue. 2016. Bat Occurrence and Habitat Preference on the Delmarva Peninsula. Northeastern Naturalist; Steuben 23:259–276.

Menzel, J. M., W. M. Ford, M. A. Menzel, Timothyc. Carter, J. E. Gardner, J. D. Garner, and J. E. Hofmann. 2005*a*. Summer habitat use and home-range analysis of the endangered Indiana bat. Journal of Wildlife Management 69:430–436.

Menzel, J. M., M. A. Menzel, J. C. Kilgo, W. M. Ford, and J. W. Edwards. 2005*b*. Bat response to Carolina bays and wetland restoration in the southeastern U.S. Coastal Plain. Wetlands 25:542–550.

Michaels, D. 2019. Deadly Bat Fungus Detected in California. CDFW News. <https://cdfgnews.wordpress.com/2019/07/05/deadly-bat-fungus-detected-in-california/>. Accessed 23 Oct 2019.

Millon, L., C. Colin, F. Brescia, and C. Kerbiriou. 2018. Wind turbines impact bat activity, leading to high losses of habitat use in a biodiversity hotspot. Ecological Engineering 112:51–54.

Moore, M. J., D. J. Orth, and E. A. Frimpong. 2017. Occupancy and detection of clinch dace using two gear types. Journal of Fish and Wildlife Management 8:530–543.

Moosman, P. R., J. P. Veilleux, G. W. Pelton, and H. H. Thomas. 2013. Changes in capture rates in a community of bats in New Hampshire during the progression of white-nose syndrome. Northeastern Naturalist 20:552–558.

Murray, K. L., E. R. Britzke, B. M. Hadley, and L. W. Robbins. 1999. Surveying bat communities: a comparison between mist nets and the Anabat II bat detector system. Acta chiropterologica 1:105–112.

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

Muthersbaugh, M. S., W. M. Ford, A. Silvis, and K. E. Powers. 2019*b*. Activity patterns of cave-dwelling bat species during pre-hibernation swarming and post-hibernation emergence in the central Appalachians. Diversity-Basel 11:159.

Niver, R., A. King, M. P. Armstrong, and W. M. Ford. 2014. Methods to evaluate and develop minimum recommended summer survey effort for Indiana bats: White paper. U.S. Fish and Wildlife Service. <https://www.fws.gov/midwest/endangered/mammals/inba/surveys/pdf/WhitePaperIBatSurveyEffort13Jan2014.pdf>. Accessed 27 Feb 2017.

Nocera, Tomás, W. M. Ford, A. Silvis, and C. A. Dobony. 2019. Patterns of acoustical activity of bats prior to and 10 years after WNS on Fort Drum Army Installation, New York. Global Ecology and Conservation 18:e00633.

Nocera, Tomas, W. M. Ford, A. Silvis, and C. A. Dobony. 2019. Let’s agree to disagree: comparing auto-acoustic identification programs for Northeastern bats. Journal of Fish and Wildlife Management.

Norberg, U. M., and J. M. V. Rayner. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London. B, Biological Sciences 316:335–427.

Norquay, K. J. O., F. Martinez-Nuñez, J. E. Dubois, K. M. Monson, and C. K. R. Willis. 2013. Long-distance movements of little brown bats (*Myotis lucifugus*). Journal of Mammalogy 94:506–515.

O'Connor, K. M., L. R. Nathan, M. R. Liberati, M. W. Tingley, J. C. Vokoun, and T. A. G. Rittenhouse. 2017. Camera trap arrays improve detection probability of wildlife: Investigating study design considerations using an empirical dataset. PLoS ONE 12.

O'Farrell, M. J., and W. L. Gannon. 1999. A comparison of acoustic versus capture techniques for the inventory of bats. Journal of Mammalogy 80:24–30.

O'Keefe, J. M., S. C. Loeb, H. S. Hill Jr., and J. Drew Lanham. 2014. Quantifying clutter: A comparison of four methods and their relationship to bat detection. Forest Ecology and Management 322:1–9.

Omernik, J. M. 1987. Map Supplement: Ecoregions of the Conterminous United States. Annals of the Association of American Geographers 77:118–125.

Otto, C. R. V., and G. J. Roloff. 2011. Using Multiple Methods to Assess Detection Probabilities of Forest-Floor Wildlife. Journal of Wildlife Management 75:423–431.

Owen, S. F., M. A. Menzel, J. W. Edwards, W. M. Ford, J. M. Menzel, B. R. Chapman, P. B. Wood, and K. V. Miller. 2004. Bat activity in harvested and intact forest stands in the Allegheny mountains. Northern Journal of Applied Forestry 21:154–159.

Patriquin, K. J., and R. M. R. Barclay. 2003. Foraging by bats in cleared, thinned and unharvested boreal forest. Journal of Applied Ecology 40:646–657.

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 122:4757.

Pettit, J. L., and J. M. O'Keefe. 2017. Impacts of White-Nose Syndrome Observed During Long-Term Monitoring of a Midwestern Bat Community. Journal of Fish and Wildlife Management 8:69–78.

Powers, K. E., R. J. Reynolds, W. Orndorff, W. M. Ford, and C. S. Hobson. 2015. Post-White-nose syndrome trends in Virginias cave bats, 2008-2013. Journal of Ecology and The Natural Environment 7:113–123.

Pregler, K., J. Vokoun, T. Jensen, and N. Hagstrom. 2015. Using Multimethod Occupancy Estimation Models to Quantify Gear Differences in Detection Probabilities: Is Backpack Electrofishing Missing Occurrences for a Species of Concern? Transactions of the American Fisheries Society 144.

Reichert, B., C. L. Lausen, C. Corben, K. Livengood, J. Szewczak, T. Weller, S. C. Loeb, R. Rodriguez, T. Hohoff, J. Siemers, B. Burkholder, and C. Herzog. 2017. NABat guide to acoustic detectors settings v1.0.

Robbins, L. W., K. L. Murray, and P. M. McKenzie. 2008. Evaluating the effectiveness of the standard mist-netting protocol for the endangered Indiana bat (*Myotis sodalis*). Northeastern Naturalist 15:275–282.

Rockey, C. D., J. P. Stumpf, and A. Kurta. 2013. Additional winter recoveries of Indiana bats (*Myotis sodalis*) banded during summer in Michigan. Northeastern Naturalist 20:N8–N13.

Russo, D., and C. C. Voigt. 2016. The use of automated identification of bat echolocation calls in acoustic monitoring: A cautionary note for a sound analysis. Ecological Indicators 66:598–602.

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

Schirmacher, M. R., S. B. Castleberry, W. M. Ford, and K. V. Miller. 2007. Habitat associations of bats in south-central West Virginia. Proceedings of the Annual Conference of the southeastern association of fish and wildlife agencies. 61:46-52. 61. <https://www.fs.usda.gov/treesearch/pubs/17269>. Accessed 17 Oct 2019.

Seibold, S., J. Buchner, C. Bässler, and J. Müller. 2013. Ponds in acidic mountains are more important for bats in providing drinking water than insect prey. Journal of Zoology 290:302–308.

Silvis, A., W. M. Ford, E. R. Britzke, N. R. Beane, and J. B. Johnson. 2012. Forest succession and maternity day roost selection by *Myotis septentrionalis* in a mesophytic hardwood forest. International Journal of Forestry Research 2012:e148106.

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 97:1565–1577.

Song Meter SM3BAT bioacoustics recorder user guide. 2018. User Manual, Wildlife Acoustics, Inc., Maynard, MA.

Sparks, D. W., C. M. Ritzi, J. E. Duchamp, and J. O. Whitaker. 2005. Foraging habitat of the Indiana bat (*Myotis sodalis*) at an urban-rural interface. Journal of Mammalogy 86:713–718.

Sprong, L., M. Keith, and E. Seamark. 2012. Assessing the effect of waterproofing on three different bat detectors. African Bat Conservation News 28:4–14.

St. Germain, M. J., A. B. Kniowski, A. Silvis, and W. M. Ford. 2017. Who knew? First *Myotis sodalis* (Indiana Bat) maternity colony in the Coastal Plain of Virginia. Northeastern Naturalist 24:N5–N10.

Starbuck, C. A., S. K. Amelon, and F. R. Thompson. 2015. Relationships between bat occupancy and habitat and landscape structure along a savanna, woodland, forest gradient in the Missouri Ozarks. Wildlife Society Bulletin 31:20–30.

Teets, K. D., S. C. Loeb, and D. S. Jachowski. 2019. Detection probability of bats using active versus passive monitoring. Acta Chiropterologica 21:205–213.

Thogmartin, W. E., R. A. King, P. C. McKann, J. A. Szymanski, and L. Pruitt. 2012. Population-level impact of White-nose Syndrome on the endangered Indiana bat. Journal of Mammalogy 93:1086–1098.

Thogmartin, W. E., C. A. Sanders-Reed, J. A. Szymanski, P. C. McKann, L. Pruitt, R. A. King, M. C. Runge, and R. E. Russell. 2013. White-nose Syndrome is likely to extirpate the endangered Indiana bat over large parts of its range. Biological Conservation 160:162–172.

Timpone, J., K. E. Francl, D. Sparks, V. B. Jr, and J. Beverly. 2011. Bats of the Cumberland Plateau and Ridge and Valley Provinces, Virginia. Southeastern Naturalist 10:515–528.

Tobin, B., and D. Weary. 2004. Digital engineering aspects karst map: a GIS version of Davies, W.E.; Simpson, J.H.; Ohlmacher, G.C.; Kirk, W.S.; and Newton, E.G., 1984, Engineering Aspects of Karst: U.S. Geological Survey, National Atlas of the United States, scale 1:7,500,000. Open-File Report OF-2004-1352, U.S. Geological Survey. <http://pubs.usgs.gov/of/2004/1352/>.

Turner, G., D. Reeder, and J. Coleman. 2011. A Five-year Assessment of Mortality and Geographic Spread of White-Nose Syndrome in North American Bats, with a Look at the Future. Update of White-Nose Syndrome in Bats. Bat Research News 52:13–27.

US Environmental Protection Agency. 2013. Level III Ecoregions of the Conterminous United States. U.S. EPA Office of Research and Development - National Health and Environmental Effects Research Laboratory, Corvallis, OR. <https://www.epa.gov/eco-research/level-iii-and-iv-ecoregions-continental-united-states>.

U.S. Fish and Wildlife Service [USFWS]. 2009. Indiana bat 5-year review: Summary and evaluation. Bloomington Ecological Services Office, Bloomington, Indiana. <https://www.fws.gov/northeast/nyfo/es/FINAL%20IBat%205-YR%20Review%20093009.pdf>. Accessed 10 Sep 2019.

U.S. Fish and Wildlife Service [USFWS]. 2015. Indiana Bat Range Map and Recovery Units. <https://www.fws.gov/midwest/Endangered/mammals/inba/RangeMapINBA.html>. Accessed 10 Aug 2019.

U.S. Fish and Wildlife Service [USFWS]. 2019*a*. Rangewide Indiana bat summer survey guidance. <http://www.fws.gov/midwest/Endangered/mammals/inba/inbasummersurveyguidance.html>. Accessed 13 Sep 2015.

U.S. Fish and Wildlife Service [USFWS]. 2019*b*. Indiana bat summer survey guidance: Automated acoustic bat id software programs. <https://www.fws.gov/midwest/endangered/mammals/inba/surveys/inbaAcousticSoftware.html>. Accessed 7 Aug 2019.

Virginia Department of Game and Inland Fisheries. 2019. Fish and Wildlife Information Service. <https://vafwis.dgif.virginia.gov/fwis/>. Accessed 30 Oct 2019.

Voigt, C. C., K. Schneeberger, S. L. Voigt-Heucke, and D. Lewanzik. 2011. Rain increases the energy cost of bat flight. Biology Letters 7:793–795.

Waters, D. A., and A. L. Walsh. 1994. The influence of bat detector brand on the quantitative estimation of bat activity. Bioacoustics 5:205–221.

Wei, T., and V. Simko. 2017. R package “corrplot”: Visualization of a Correlation Matrix. <https://CRAN.R-project.org/package=corrplot>. Accessed 18 Aug 2019.

Weller, T. J., and J. A. Baldwin. 2012. Using echolocation monitoring to model bat occupancy and inform mitigations at wind energy facilities. The Journal of Wildlife Management 76:619–631.

Weller, T. J., and C. J. Zabel. 2002. Variation in bat detections due to detector orientation in a forest. Wildlife Society Bulletin 30:922–930.

White-Nose Syndrome Response Team. 2019. White-nose syndrome spread maps. <https://www.whitenosesyndrome.org/static-page/wns-spread-maps>. Accessed 31 Oct 2019.

Wolcott, K. A., and K. Vulinec. 2012. Bat activity at woodland/farmland interfaces in central Delaware. Northeastern Naturalist 19:87–98.

Yates, M. D., and R. M. Muzika. 2006. Effect of forest structure and fragmentation on site occupancy of bat species in Missouri Ozark forests. Journal of Wildlife Management 70:1238–1248.

Table 7. Recording settings for bat acoustic detectors used when comparing detector types at Fort Knox, KY, May-August 2017.

Setting	**Song Meter SM3BAT FS**	**Song Meter SM3BAT ZC**	**Pettersson D500X FS**	**AnaBat SD2 ZC**	**AnaBat Swift FS**
Sampling Rate	384 kHz	NA	500 kHz	NA	320 kHz
Division Ratio	--	8	--	8	--
Gain	Automatic	Automatic	80	6	--
Min frequency	16 kHz	16 kHz	--	--	16 kHz
Max frequency	192 kHz	192 kHz	--	--	250 kHz
High pass filter	16 kHz	16 kHz	ON	--	--
Trigger level	Automatic	Automatic	80	--	Sensitivity: 12
Trigger min	Dmin: 1.5 ms	Dmin: 1.5 ms	TS: Med	--	1 ms
Trigger max	Dmax: off	Dmax: off	--	--	--
Recording window	Trgwin: 3 s	Trgwin: 3 s	LEN: 3 s	--	3 s
Max file time	Trgmax: 15 s	Trgmax: 15 s		--	15 s
File interval	--	--	0	--	--
Pretrigger	--	--	OFF	--	--
Auto Record	--	--	YES	--	--
Installed memory capacity	128 GB	8 GB	128 GB	4 GB	128 GB

Table 8. Variables used in candidate models for nightly bat activity and detection probability from acoustic sampling sites at Fort Knox, KY, May- August 2017. Date only used in bat activity models.

Variable	**Description**	**Type**
Wind	Mean nightly wind speed	Continuous
Precipitation	Proportion of night hours with measureable precipitation	Continuous
Detector	Type of acoustic detector and recording method	Categorical
Site	One of nine	Categorical
Date	Day of the year	Continuous

Table 9. Summary of data collected by five bat acoustic detector- recording style combinations including total number of number of nights with presence for Indiana (*Myotis sodalis*; MYSO), eastern red (*Lasiurus borealis*; LABO) and big brown (*Eptesicus fuscus*; EPFU) bats and total call files for high-, mid-, and low-frequency phonic groups from acoustic sampling sites at Fort Knox, KY, May- August 2017.

			Nights with presence			**Number of call files**		
Detector	**Sites**	**Nights**	**MYSO**	**LABO**	**EPFU**	**High**	**Mid**	**Low**
Anabat SD2	6	153	13	102	56	4077	4236	6047
SM3BAT FS	8	161	65	139	138	5145	9997	13561
SM3BAT ZC	8	161	42	99	117	2168	4465	8392
D500X	6	107	26	68	62	1065	3793	2156
Anabat Swift	8	217	52	132	146	2440	6174	8909

Table 10. Rankings of single-season occupancy models predicting Indiana bat (*Myotis sodalis*), eastern red bat (*Lasiurus borealis*), and big brown bat (*Eptesicus fuscus*) detection probability from eight acoustic monitoring sites with 799 detector nights at Fort Knox, KY, May- August 2017.

Model	**K**	**AICc**	**ΔAICc**	ω_i
Indiana bat				
Detector + Wind	7	565.32	0.00	0.40
Detector	6	565.75	0.43	0.33
Detector + Precipitation + Wind	8	567.31	1.99	0.15
Detector + Precipitation	7	567.75	2.43	0.12
Null	2	643.60	78.28	0.00
Wind	3	644.74	79.42	0.00
Precipitation	3	645.50	80.18	0.00
Eastern red bat				
Detector	6	960.38	0.00	0.31
Detector + Wind	7	960.54	0.16	0.29
Detector + Precipitation	7	961.00	0.62	0.23
Detector + Precipitation + Wind	8	961.53	1.15	0.18
Null	2	990.08	29.70	0.00
Precipitation	3	990.69	30.31	0.00
Wind	3	990.87	30.49	0.00
Big brown bat				
Detector + Precipitation + Wind	8	901.90	0.00	0.59
Detector + Wind	7	904.12	2.22	0.19
Detector + Precipitation	7	904.25	2.35	0.18
Detector	6	907.62	5.72	0.03
Precipitation	3	965.97	64.07	0.00
Wind	3	967.88	65.98	0.00
Null	2	968.94	67.04	0.00

Table 11. Model coefficients, standard errors (SE), and 95% upper and lower confidence intervals (CI) for variables in competing occupancy models predicting detection probability of Indiana bats (*Myotis sodalis*) from eight acoustic monitoring sites with 799 detector nights at Fort Knox, KY, May-August 2017.

Model and variables	**Coefficient**	**SE**	**Lower CI**	**Upper CI**
Detector + Wind				
Intercept (Anabat SD2)	-1.94	0.32	-2.56	-1.32
Song Meter SM3BAT FS	3.18	0.41	2.38	3.99
Song Meter SM3BAT ZC	1.90	0.39	1.15	2.66
Petterson D500X	1.33	0.40	0.55	2.11
Anabat Swift	1.80	0.37	1.08	2.52
Wind	-0.17	0.11	-0.38	0.04
Detector				
Intercept (Anabat SD2)	-1.91	0.31	-2.52	-1.29
Song Meter SM3BAT FS	3.14	0.41	2.34	3.94
Song Meter SM3BAT ZC	1.86	0.38	1.11	2.61
Petterson D500X	1.30	0.40	0.52	2.07
Anabat Swift	1.78	0.37	1.06	2.50
Detector + Precipitation + Wind				
Intercept (Anabat SD2)	-1.94	0.32	-2.56	-1.32
Song Meter SM3BAT FS	3.19	0.41	2.38	4.00
Song Meter SM3BAT ZC	1.90	0.39	1.15	2.66
Petterson D500X	1.33	0.40	0.55	2.11
Anabat Swift	1.80	0.37	1.08	2.52
Wind	0.01	0.12	-0.22	0.25
Precipitation	-0.17	0.11	-0.38	0.04

Table 12. Model estimate, standard errors (SE), and 95% upper and lower confidence intervals (CI) for variables in competing occupancy models predicting detection probability of eastern red bats (*Lasiurus borealis*) from eight acoustic monitoring sites with 799 detector nights at Fort Knox, KY, May-August 2017.

Model and variables	Coefficient	SE	Lower CI	Upper CI
Detector				
Intercept (Anabat SD2)	0.69	0.17	0.36	1.03
Song Meter SM3BAT FS	1.15	0.29	0.59	1.71
Song Meter SM3BAT ZC	-0.23	0.24	-0.69	0.24
Petterson D500X	0.27	0.29	-0.29	0.84
Anabat Swift	-0.25	0.22	-0.69	0.18
Detector + Wind				
Intercept (Anabat SD2)	0.69	0.17	0.35	1.02
Song Meter SM3BAT FS	1.17	0.29	0.61	1.73
Song Meter SM3BAT ZC	-0.21	0.24	-0.67	0.25
Petterson D500X	0.28	0.29	-0.29	0.84
Anabat Swift	-0.25	0.22	-0.69	0.18
Wind	-0.11	0.08	-0.26	0.05
Detector + Precipitation				
Intercept (Anabat SD2)	0.69	0.17	0.36	1.03
Song Meter SM3BAT FS	1.15	0.29	0.59	1.71
Song Meter SM3BAT ZC	-0.23	0.24	-0.69	0.23
Petterson D500X	0.26	0.29	-0.30	0.83
Anabat Swift	-0.26	0.22	-0.69	0.18
Precipitation	-0.09	0.08	-0.24	0.06

Table 13. Model coefficients, standard errors (SE), and 95% upper and lower confidence intervals (CI) for variables in best supported occupancy model predicting detection probability of big brown bats (*Eptesicus fuscus*) from eight acoustic monitoring sites with 799 detector nights at Fort Knox, KY, May-August 2017.

Variables	Coefficient	SE	Lower CI	Upper CI
Intercept (Anabat SD2)	-0.25	0.18	-0.60	0.11
Song Meter SM3BAT FS	2.07	0.29	1.50	2.64
Song Meter SM3BAT ZC	1.57	0.27	1.04	2.10
Petterson D500X	0.57	0.27	0.05	1.10
Anabat Swift	0.96	0.23	0.51	1.42
Precipitation	-0.17	0.08	-0.33	-0.01
Wind	-0.17	0.08	-0.33	-0.01

Table 14. Competing, best supported, and null generalized linear mixed models predicting high frequency, mid frequency, and low frequency acoustically recorded nightly bat activity from eight monitoring sites with 799 detector nights at Fort Knox, KY, May- August 2017.

Model	**K**	**AICc**	**ΔAICc**	ω_i
High frequency				
Detector + Wind + Date	9	5356.27	0.00	0.64
Null	3	5605.52	249.25	<0.001
Mid frequency				
Detector + Wind + Precipitation	9	6660.68	0.00	0.24
Detector + Wind	8	6660.74	0.06	0.23
Detector + Wind + Date + Precipitation	10	6661.06	0.38	0.20
Detector + Wind + Date	9	6661.85	1.18	0.13
Detector + Date + Precipitation	9	6662.28	1.61	0.11
Null	3	6900.43	239.75	<0.001
Low frequency				
Detector	7	7137.90	0.00	0.35
Detector + Date	8	7138.97	1.08	0.20
Detector + Wind	8	7139.73	1.83	0.14
Null	3	7183.37	45.48	<0.001

Table 15. Model estimates, standard errors (SE), and 95% upper and lower confidence intervals (CI) for variables in best supported model predicting recorded nightly activity of bats in the high frequency phonic group from eight acoustic monitoring sites with 799 detector nights at Fort Knox, KY, May-August 2017.

Variables	**Estimate**	**SE**	**Lower CI**	**Upper CI**
Intercept (Anabat SD2)	2.35	0.37	1.63	3.08
Day	0.40	0.10	0.20	0.60
Song Meter SM3BAT FS	0.64	0.10	0.44	0.84
Song Meter SM3BAT ZC	-0.37	0.10	-0.57	-0.17
Pettersson D500X	-0.94	0.11	-1.16	-0.73
Anabat Swift	-0.57	0.09	-0.75	-0.39
Wind	0.08	0.03	0.01	0.14

Table 16: Model estimates, standard errors (SE), and 95% upper and lower confidence intervals (CI) for variables in selected competing models predicting recorded nightly activity of bats in the mid frequency phonic group from eight acoustic monitoring sites with 799 detector nights at Fort Knox, KY, May-August 2017.

Model and variables	**Estimate**	**SE**	**Lower CI**	**Upper CI**
Detector + Wind				
Intercept (Anabat SD2)	2.51	0.45	1.63	3.40
Song Meter SM3BAT FS	1.44	0.11	1.23	1.66
Song Meter SM3BAT ZC	0.35	0.11	0.14	0.57
Petterson D500X	0.02	0.13	-0.23	0.27
Anabat Swift	0.12	0.10	-0.08	0.32
Wind	0.08	0.03	0.01	0.14
Detector + Wind + Date + Precipitation				
Intercept (Anabat SD2)	2.54	0.44	1.68	3.39
Date	-0.15	0.11	-0.37	0.07
Song Meter SM3BAT FS	1.42	0.11	1.20	1.64
Song Meter SM3BAT ZC	0.33	0.11	0.11	0.55
Petterson D500X	0.01	0.13	-0.24	0.26
Anabat Swift	0.12	0.10	-0.08	0.33
Wind	0.06	0.03	-0.01	0.13
Precipitation	0.06	0.04	-0.01	0.13

Table 17. Model estimates, standard errors (SE), and 95% upper and lower confidence intervals (CI) for variables in competing models predicting recorded nightly activity of bats in the low frequency phonic group from eight acoustic monitoring sites with 799 detector nights at Fort Knox, KY, May – August 2017.

Model and variables	**Estimate**	**SE**	**Lower CI**	**Upper CI**
Detector				
Intercept (Anabat SD2)	3.55	0.39	2.80	4.31
Song Meter SM3BAT FS	0.22	0.16	-0.09	0.53
Song Meter SM3BAT ZC	-0.40	0.16	-0.71	-0.09
Petterson D500X	-0.79	0.19	-1.15	-0.42
Anabat Swift	-0.51	0.15	-0.81	-0.21
Detector + Date				
Intercept (Anabat SD2)	3.60	0.36	2.88	4.31
Date	-0.13	0.13	-0.40	0.13
Song Meter SM3BAT FS	0.18	0.16	-0.14	0.50
Song Meter SM3BAT ZC	-0.44	0.16	-0.76	-0.11
Petterson D500X	-0.82	0.19	-1.19	-0.45
Anabat Swift	-0.54	0.15	-0.84	-0.23
Detector + Wind				
Intercept (Anabat SD2)	3.55	0.39	2.79	4.30
Song Meter SM3BAT FS	0.23	0.16	-0.09	0.54
Song Meter SM3BAT ZC	-0.38	0.16	-0.70	-0.07
Petterson D500X	-0.78	0.19	-1.14	-0.42
Anabat Swift	-0.51	0.15	-0.80	-0.21
Wind	-0.02	0.04	-0.10	0.06

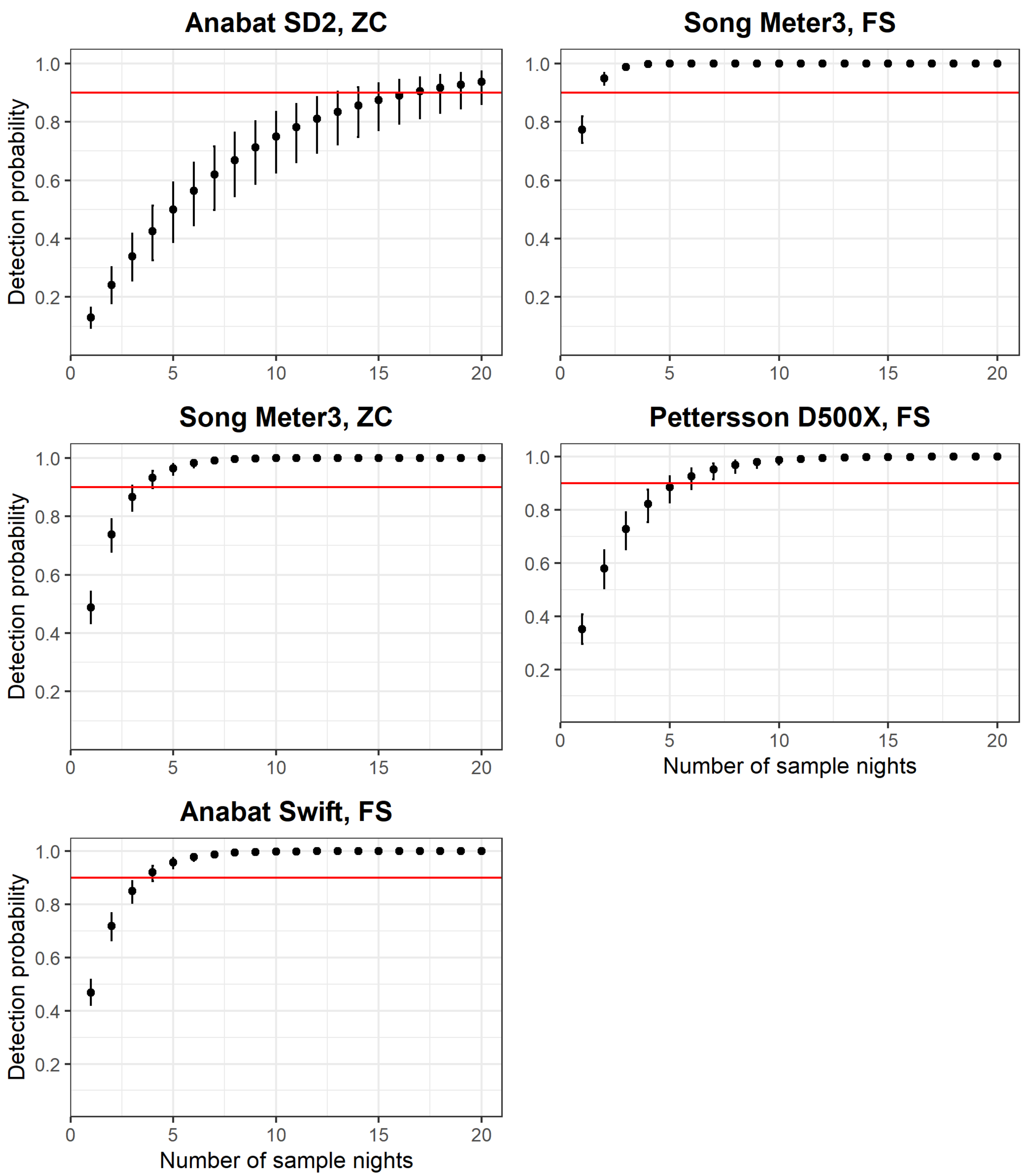

Figure 7. Predicted cumulative detection probability curves for Indiana bats (*Myotis sodalis*) with standard errors for four different acoustic detector brands and both full spectrum (FS) and zero crossing (ZC) recording styles. Red line represents a 90% probability of detecting a bat given that it is present at an acoustic monitoring site. Data from five acoustic monitoring sites with 529 detector nights at Fort Knox, KY, May – August 2017.

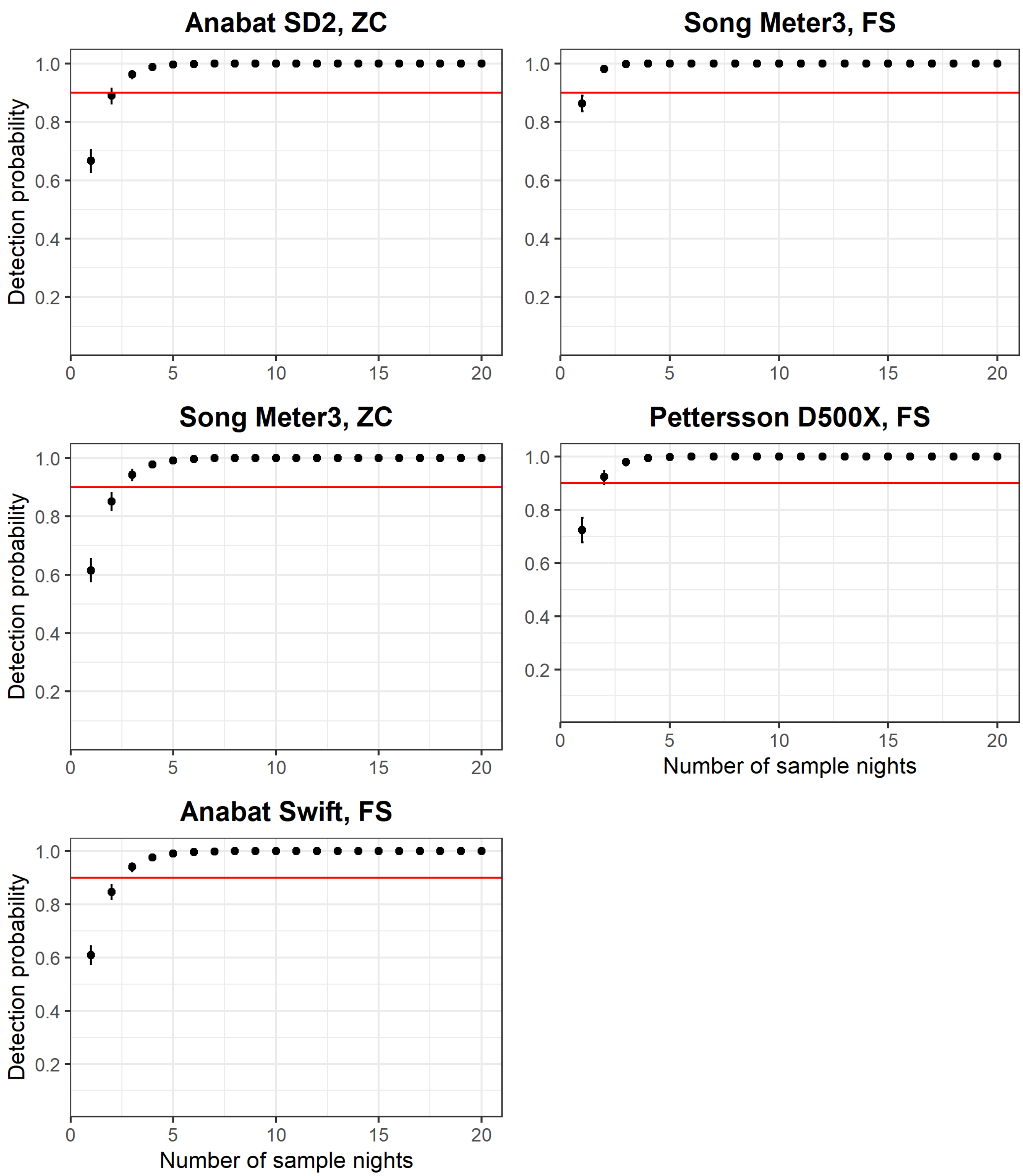

Figure 8. Predicted cumulative detection probability curves for eastern red bats (*Lasiurus borealis*) with standard errors for four different acoustic detector brands and both full spectrum (FS) and zero crossing (ZC) recording styles. Red line represents a 90% probability of detecting a bat given that it is present at an acoustic monitoring site. Data from eight acoustic monitoring sites with 799 detector nights at Fort Knox, KY, May – August 2017.

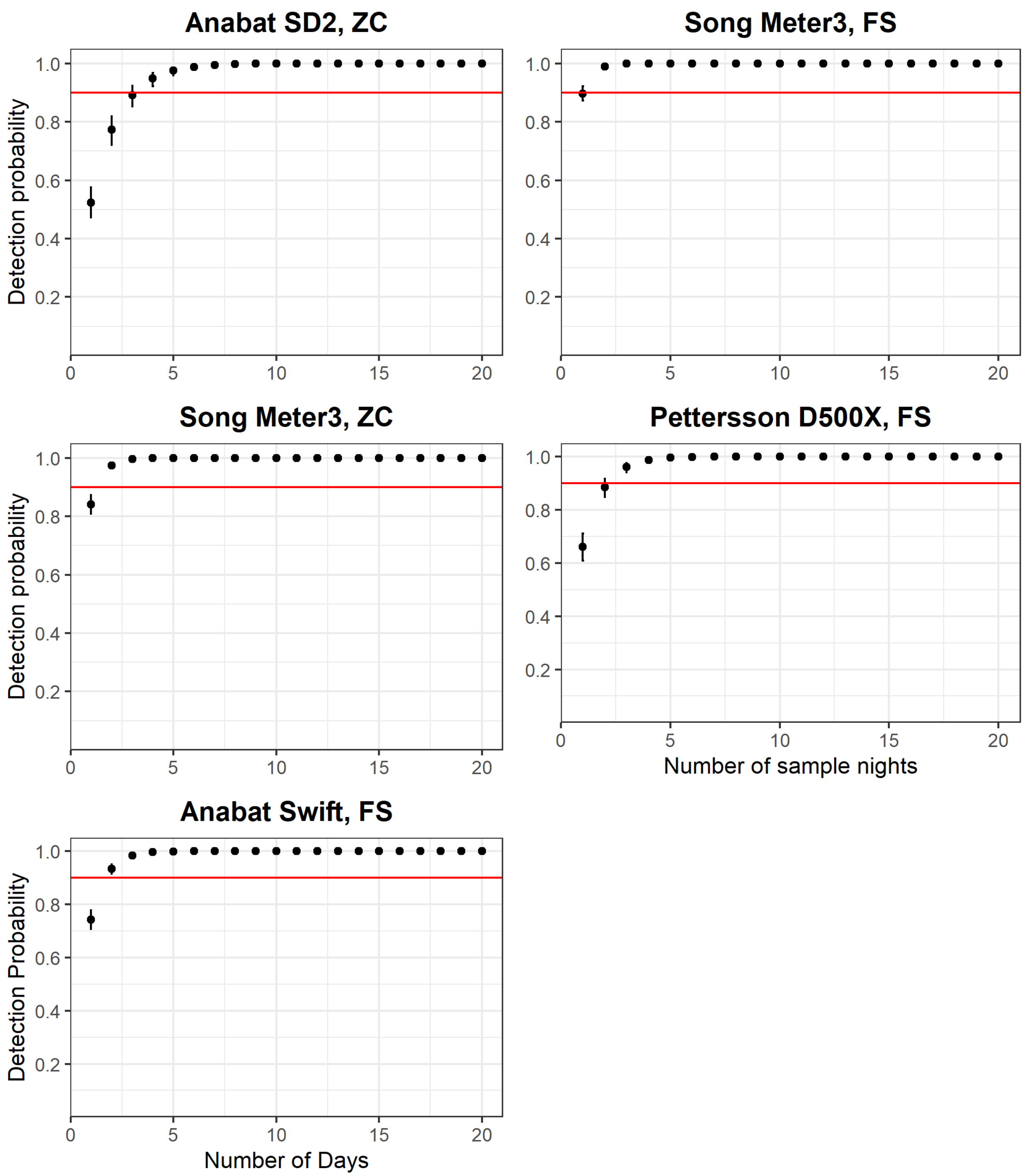

Figure 9. Predicted cumulative detection probability curves big brown bats (*Eptesicus fuscus*) with standard errors for four different acoustic detector brands and both full spectrum (FS) and zero crossing (ZC) recording syles. Red line represents a 90% probability of detecting a bat given that it is present at an acoustic monitoring site. Data from eight acoustic monitoring sites with 799 detector nights at Fort Knox, KY, May – August 2017.

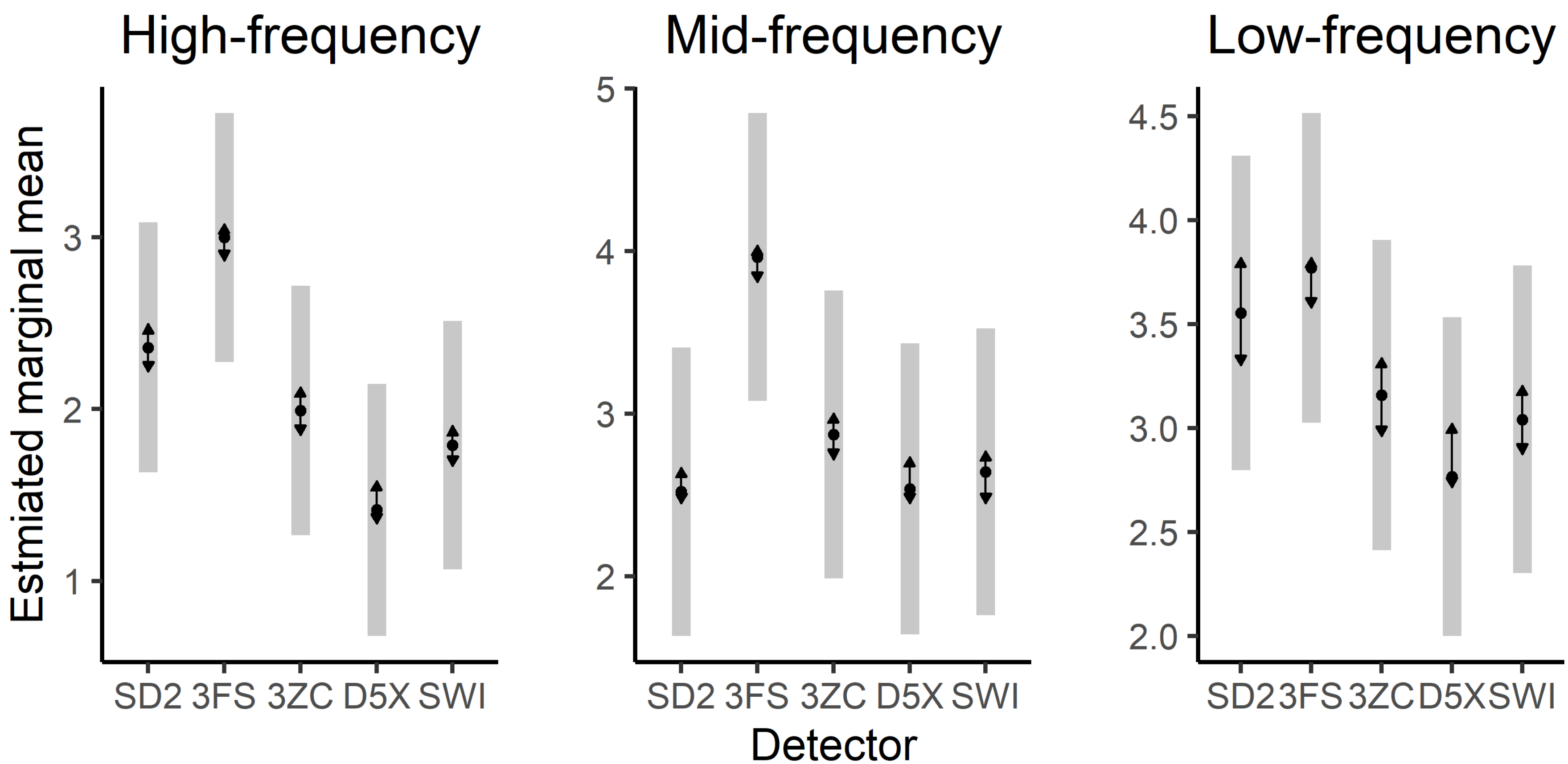

Figure 10. Results of *post-hoc* pairwise comparisons of estimated marginal means from GLMM predicting bat acoustic call files per night by detector type: Anabat SD2 (SD2), Song Meter SM3BAT in full spectrum (3FS) and zero-crossing (3ZC), Pettersson D500X (D5X), and Anabat Swift (SWI). Grey bars represent confidence intervals, and arrows illustrate pairwise post-hoc comparisons among detectors. If an arrow from one detector overlaps an arrow from another, the difference is not statistically significant. Total site-nights surveyed by detector type ranged from 107-217 detector-nights across eight acoustic monitoring sites with 799 total detector nights at Fort Knox, KY, May – August 2017.