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Factors Affecting the Probability of Acoustic Detection and Site Occupancy of Bats in Central Indiana

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FACTORS AFFECTING THE PROBABILITY OF ACOUSTIC DETECTION AND SITE OCCUPANCY OF BATS IN CENTRAL INDIANA

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ABSTRACT

Documenting the presence of rare bat species can be difficult. The current summer survey protocol for the federally endangered Indiana bat (*Myotis sodalis*) requires passive acoustic sampling with directional microphones (e.g., Anabats), but there are still questions about best practices for choosing survey sites and appropriate detector models. Indiana bats are capable of foraging in an array of cover types, including structurally-complex, interior forests. Further, data acquisition among different commercially available bat detectors is likely highly variable, due to the use of proprietary microphones with different frequency responses, sensitivities, and directionality. We paired omnidirectional Wildlife Acoustic SM2BAT+ (SM2) and directional Titley Scientific Anabat SD2 (Anabat) detectors at 71 random points near Indianapolis, Indiana from May-August 2012-2013 to compare data acquisition by phonic group (low, mid, *Myotis*) and to determine what factors affect probability of detection and site occupancy for Indiana bats when sampling with acoustics near an active maternity colony (0.20-8.39 km away). Weatherproofing for Anabat microphones was 45° angle PVC tubes and for SM2 microphones was their foam shielding; microphones were paired at 2 m and 5 m heights. Habitat and landscape covariates were measured in the field or via ArcGIS. We adjusted file parameters to make SM2 and Anabat data comparable. Files were identified using Bat Call ID software, with visual inspection of Indiana bat calls. The effects of detector type, phonic group, height, and their interactions on mean files recorded per site were assessed using generalized estimating equations and LSD pairwise comparisons. We reduced probability of detection (p) and site occupancy (ψ)

model covariates with Pearson’s correlation and PCA. We used Presence 6.1 software and Akaike’s Information Criteria to assess models for p and ψ. Anabats and SM2s did not perform equally. Anabats recorded more low and midrange files, but fewer *Myotis* files per site than SM2s. When comparing the same model of detectors, deployment height did not impact data acquisition. Weatherproofing may limit the ability of Anabats to record *Myotis*, but Anabat microphones may have greater detection ranges for low and midrange bats. Indiana bat detections were low for both detector types, representing only 4.4% of identifiable bat files recorded by SM2s. We detected Indiana bats at 43.7% of sampled sites and on 31.4% of detector-nights; detectability increased as “forest closure” and mean nightly temperature increased, likely due to reduced clutter and increased bat activity, respectively. Proximity to colony trees and specific cover types generally did not affect occupancy, suggesting that Indiana bats use a variety of cover types in this landscape. Omnidirectional SMX-US microphones may be more appropriate for Indiana bat surveys than directional Anabat microphones. However, we conclude that 2 nights of passive acoustic sampling per site may be insufficient for reliably detecting this species when it is present. In turn, the use of acoustic monitoring as a means to document presence or probable absence should be reassessed.

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DIFFERENCES IN DATA ACQUISTION WITH PAIRED BAT DETECTORS IN FIELD SETTINGS

INTRODUCTION

Insectivorous bats of eastern North America are nocturnal, volant and exceptionally agile in cluttered landscapes; consequently, these small mammals are extremely difficult to study. Capture techniques (e.g., mist-netting), which are labor-intensive and oftentimes low-yielding, have traditionally provided biologists with information about the presence or absence of bat species within particular habitats (Kunz and Kurta 1988, O'Farrell and Gannon 1999). However, with population declines of many bat species across North America due to habitat loss and degradation (Weller et al. 2009), wind-energy related fatalities (Kunz et al. 2007), and the white-nose syndrome fungal disease (Frick et al. 2010, Turner et al. 2011), sampling via capture techniques may become increasingly ineffective. Ultrasonic bat detector technologies provide viable alternatives (Murray et al. 1999, O'Farrell and Gannon 1999, Armitage and Ober 2010). Bat detectors sample larger areas and often record higher species richness than capture techniques alone (Murray et al. 1999, O'Farrell and Gannon 1999). Furthermore, certain bat detector models can record autonomously (Miller 2001), which allows numerous areas to be sampled simultaneously with minimal effort (Gorresen et al. 2008).

Accordingly, acoustic monitoring via bat detectors has become a popular research method; however, limitations of this sampling technique, if not addressed, may result in incorrect conclusions and hinder proper management decisions.

Acoustic bat detectors suffer from unavoidable sampling biases (Murray et al. 1999, O'Farrell and Gannon 1999, Hayes 2000). Bat detectors sample finite airspaces; thus, only a limited area exists in which echolocating bats will be detected (Limpens and McCracken 2004). The size of the airspace a bat detector samples (henceforth, "sampling area") is a function of microphone design and local recording conditions. Sampling areas are dictated by the microphone's sensitivity (Larson and Hayes 2000), frequency response (Waters and Walsh 1994, Adams et al. 2012), directionality (Downes 1982, Waters and Walsh 1994, Limpens and McCracken 2004), and weatherproofing (Britzke et al. 2010), as well as environmental factors that impact the transmission of sound waves through air (Limpens and McCracken 2004). Climatic conditions influence the rate at which sound attenuates in air (Griffin 1971, Lawrence and Simmons 1982, Petterson 2004), which thereby impacts the size of the sampling area. Clutter (e.g., vegetation) creates interference (Schnitlzer and Kalko 2001, Broders et al. 2004, Obrist et al. 2011) by refracting, reflecting, or scattering ultrasounds (Pettersson 2004), and the orientation of the microphone in relation to clutter affects the size of the sampling area (Limpens and McCracken 2004). Detectors deployed in uncluttered environments have larger sampling areas and record higher relative bat activity than detectors placed near vegetation (Weller and Zabel 2002).

The data acquisition abilities of bat detectors are dictated by relationships between the microphones' sampling area and its response to varying sound-sources in dynamic environmental and atmospheric conditions (Limpens and McCracken 2004). The amount of bat activity a detector will record varies due to the amplitude, frequency, and signal type of the emitted ultrasounds (Downes 1982, Forbes and Newhook 1990, Limpens and McCracken 2004, Adams et al. 2012). High-frequency calls attenuate more rapidly and travel shorter distances in air than low-frequency calls (Lawrence and Simmons 1982, Parsons 1996, Pettersson 2004). Broadband frequency-modulated (FM) signals have lower source amplitudes and, thus, travel shorter distances than narrowband constant-frequency (CF) or quasi-constant-frequency (QCF) calls (Schnitlzer and Kalko 2001, Limpens and McCracken, 2004). Therefore, it may be more difficult to detect species that echolocate with high-frequency FM calls (e.g., *Myotis septentrionalis*) than species with low-frequency CF calls (e.g., *Lasiurus cinereus*); however, it is important to consider that detectability is largely influenced by the distance of the sound source from the microphone (Corben and Fellers 2001) due to the effects of geometric spreading and atmospheric absorption (Lawrence and Simmons 1982, Pettersson 2004).

There are several factors that affect the capabilities of bat detectors when deployed in field settings. Experiments suggest that the orientation and elevation of the microphone in relation to clutter (Weller and Zabel 2002), as well as microphone sensitivity (Waters and Walsch 1994, Larson and Hayes 2000, Adams et al. 2012) and weatherproofing (Britzke et al. 2010) influence data acquisition. While studies have shown that detectors of the same model can vary in their capabilities (Larson and Hayes

2000, Weller and Zabel 2002, Britzke et al. 2010), we still have only limited information on differences in data acquisition across different models or brands (especially those released in the last decade due to the rapid growth of the commercial market for bat detectors). Manufacturers of acoustic bat detectors use distinct hardware components, including proprietary microphones (Waters and Walsh 1994, Pettersson 2004, Adams et al. 2012). Consequently, sampling areas and detection ranges likely vary between different detector models (Parsons 1996, Adams et al. 2012) and, therefore, data acquisition will also likely vary (Waters and Walsh 1994).

To our knowledge, only a handful of studies have compared the data acquisition abilities of bat detectors produced by different manufacturers (Downes 1982, Forbes and Newhook 1990, Waters and Walsh 1994, Parsons 1996, Solick et al. 2011, Adams et al. 2012). Waters and Walsh (1994) found that detectors with greater microphone sensitivities consistently recorded more bat calls per hour and Parsons (1996) found significant differences among brands in regards to minimum and maximum detection distances. More recently, D. Solick (personal communication 2012) demonstrated that several models of full-spectrum detectors could not mimic the data acquisition abilities of an Anabat SD1 (Titley Scientific, Inc., Columbia, MO, USA), which is a frequency division detector. The differences observed were likely due to incompatible software features or microphone differences. Adams et al. (2012), using both playback studies and field recordings, determined that variation in directionality and microphone frequency responses led to performance differences among five models of modern bat detectors.

Because several of these studies compared detectors that may now be obsolete, additional research is needed to compare modern detectors.

We initiated a field study near Indianapolis, Indiana to compare data acquisition between two automated bat detectors: the Wildlife Acoustics SM2BAT+ (henceforth, “SM2”; Wildlife Acoustics, Inc., Concord, MA, USA) and Anabat SD2 (henceforth, “Anabat”; Titley Scientific, Inc., Columbia, MO, USA). We aimed to determine if these two models, when weatherproofed and deployed side-by-side in the field, would record similar numbers of echolocation files per phonic group. We deployed Anabats and SM2s in a manner typical of most long-term field studies aimed at the passive monitoring of bat communities. We chose Anabats and SM2s because, although these two models are arguably the most widely-used bat detectors for passive acoustic sampling in the United States, their microphone design and technical specifications are very different. SM2s utilize omnidirectional microphones, whereas Anabats utilize directional microphones; thus, each has a distinct sampling area attributable to microphone design and directionality. Overall, we expected that data acquisition for these detectors would be dissimilar (Waters and Walsch 1994, Adams et al. 2012). Like Weller and Zabel (2002), we also aimed to determine how microphone elevation influences data acquisition for each detector type. We expected that microphones elevated higher above understory vegetation would record more bat activity than microphones deployed nearer to the ground.

STUDY AREA

This study was conducted on 1,045 ha of property west-southwest of the Indianapolis International Airport between the cities of Mooresville and Plainfield, Indiana (Figure 1). The East Fork of White Lick Creek, an 84 km long, perennial stream, flows south through the study site (Stahl et al. 1997, Whitaker and Sparks 2004). Interstate 70 (I-70), running northeast-southwest, splits the study site into “northern” and “southern” sections, with State Road 67 forming the eastern and southern borders, and State Road 267 forming the western border (Figure 1). The study site north of I-70 is limited to a narrow, forested, riparian corridor, as the surrounding landscape is heavily developed with airport runways and busy highways to the east, a warehouse district to the west, residential subdivisions to the north, and large electrical substations and accompanying power lines to the south. Anthropogenic activity is commonplace and commercial planes fly within a few hundred meters of the canopy throughout the night. Agricultural lands dominate the study site south of I-70, although parcels of land have been permanently set aside as forested wildlife refuges, replanted wetlands or forests, or local parks available for recreation (Sparks et al. 2009). Overall, the area in and around the study site has been heavily modified by human activities and consists of numerous fragmented land-cover types, including farmland, wetlands, pasture/grasslands, residential/commercial developments, forested riparian corridors, and remnant deciduous forests.

Since 1996, the study site has been home to a long-term study of the summer foraging and roosting ecology of the federally endangered Indiana bat (*Myotis sodalis*;

Whitaker et al. 2004). From 1997-2013, nine bat species have been captured in mist-nets in the study area, including big brown bats (*Eptesicus fuscus*), silver-haired bats (*Lasionycteris noctivagans*), hoary bats (*Lasiurus cinereus*), eastern red bats (*Lasiurus borealis*), evening bats (*Nycticeius humeralis*), tri-colored bats (*Perimyotis subflavus*), northern long-eared bats (*M. septentrionalis*), little brown bats (*M. lucifugus*), and Indiana bats (Whitaker et al. 2004, O'Keefe et al. 2014).

METHODS

SITE SELECTION & DETECTOR SETUP

We combined 95% minimum convex polygons derived from foraging telemetry data collected for Indiana bats in previous years (2002-2011; Whitaker et al. unpublished data) to create a single polygon in ArcMap 10.0 (ESRI, Inc. Redlands, CA, USA) that outlined potential Indiana bat foraging habitat within our study site (Figure 1). From May-August 2012 and 2013, we deployed bat detectors to sample 71 random points within this polygon, with 35 points sampled in 2012 and 36 points sampled in 2013. We sampled in several land-cover types, including wetland/riparian areas (31% of our sampling effort), deciduous forests (28%), pasture/grasslands (21%), replanted forests <20 years old (16%), and farmlands (4%). Our sampling effort was restricted because private property and human activity is so commonplace within the study site. Therefore, we were forced to replace random points that were inaccessible (e.g., private property) or in locations where bat detector equipment was in jeopardy of being stolen/tampered with (e.g., public parks) or damaged (e.g., active cow pastures). Subsequently, we did not sample all land-cover types in proportion to their availability on the landscape.

We used omnidirectional SMX-US microphones and directional High Mount microphones with the SM2s and Anabats, respectively. To reduce sampling area variation among the four Anabat units we deployed, each season we calibrated microphones in accordance with Larson and Hayes (2000) using a constant 40 kHz tone emitted from an Anabat Chirper (Titley Scientific, Inc., Columbia, MO, USA). It was not possible to calibrate the four SM2 microphones we deployed; however, all detectors were purchased prior to beginning fieldwork in 2012, and new microphones were used each year. Anabats recorded zero-crossing data with a division ratio of 8 and sensitivity settings ranging from 5.5-6.5. SM2s recorded monaural, full-spectrum data with a bit depth of 16, a sampling rate of 384,000 kHz, and a WAC0 audio compression. The following settings were used with the SM2, trigger: trig left = 18db, trig win left = 2.0 s; gain: 48db, left microphone = +0.0db; high-pass filter: HPF left = fs/24; and low-pass filter: LPF left = OFF. We programmed detectors to passively record from pre-dusk (20:00 EDT) until post-dawn (8:00 EDT) each night for two consecutive detector-nights at each sampling point. A detector-night was defined as one uninterrupted night of recording. Data were included in our analyses only if a full detector-night of sampling was achieved, and in 2012 and 2013, we discarded 2 nights and 16 nights of sampling, respectively, due to Anabat malfunctions.

To mimic current protocols for passive acoustic monitoring studies, we used what we thought was the most popular weatherproofing solution for each detector type. We used the foam shielding included with SMX-US microphones and placed Anabat microphones in 45° angle PVC tubes (Britzke et al. 2010). To record the best calls possible, we selected a point with the least amount of clutter ≤ 25 m from the random point and oriented microphones towards potential bat flyways (Larson and Hayes 2000). From 16 May to 6 August 2012, we employed a double-observer method similar to Duchamp et al. (2006), with one SM2 and one Anabat paired and programmed to record simultaneously at each sampling site. Each microphone was connected to its respective detector with a 10 m cable and elevated 2 m on a metal post (Weller and Zabel 2002). Each Anabat microphone was positioned 15 cm above the SM2 microphone to prevent the Anabat's PVC enclosure from blocking a large portion of the SM2's sampling area. From 15 May to 7 August 2013, we used a similar setup, but we added a second SM2-Anabat pairing at 5 m above ground, again with Anabat microphones positioned 15 cm above SM2 microphones. Identical microphone orientations were used for the SM2-Anabat pairings at both 2 m and 5 m heights, and each coupling of detectors was randomly determined prior to deployment. To simplify discussion, 2 m microphone elevations will be referred to as "low" and 5 m microphone elevations will be referred to as "high."

ECHOLOCATION DATA ANALYSIS

For this study, a bat call, also referred to as a "file", is defined as a series of three or more consecutive echolocation pulses emitted by a single bat (Ford et al. 2005). A pulse is defined as a single echolocation sound wave within the larger bat call. Using WAC2WAV 3.3.0 (Wildlife Acoustics, Inc., Concord, MA, USA) software, we converted full-spectrum SM2 data to zero-crossing format with parameters identical to those of the Anabat (division ratio = 8, maximum file duration = 15 s, and minimum time between calls = 2 s). The SMX-US to UT filter was applied in WAC2WAV to achieve a flatter frequency response, as suggested by Wildlife Acoustics (personal communication 2012). We used Bat Call ID 2.5b (henceforth, "BCID"; Bat Call Identification, Inc., Kansas City, MO, USA) automated software to identify bat call files to one of three phonic groups (low, midrange, or *Myotis*; Romeling et al. 2012). The software referred to a call library for bats that occur in Indiana (1,546 calls of nine species), required a minimum pulse count of three for file identification (Romeling et al. 2012), and reported a conservative ≥ 90% group confidence level. BCID categorized files into phonic groups based on a clustering algorithm and call parameters such as duration, minimum frequency, slope at the flattest portion of the call, and frequency at the knee of the call (R. Allen, personal communication 2014; e.g., Romeling et al. 2012). The low phonic group (minimum call frequencies <30 kHz) contained *E. fuscus*, *L. noctivagans*, and *L. cinereus*; the midrange phonic group (non-*Myotis* bats with minimum frequency >30, but less than 50 kHz) contained *L. borealis, N. humeralis*, and *P. subflavus*; and the *Myotis* phonic group (minimum call frequencies between 30-60kHz) contained *M. lucifugus*, *M. septentrionalis,* and *M. sodalis* (Romeling et al. 2012). We excluded *M. leibii* and *M. grisescens* from BCID analyses because these species have not been captured with mist-nets in the study site over the past 15 years (Whitaker et al. 2006, J. O'Keefe, personal communication 2012). We overlooked files that could not be identified to phonic group by BCID due to insufficient pulse counts or poor call quality. For SM2s, 51.7% of all files recorded in 2012 were unidentifiable by BCID, while 43.1% could not be identified in 2013. For Anabats, 44.6 % of recorded files were unidentifiable by BCID in 2012, while 38.6% could not be identified in 2013. These percentages do not include non-bat files (e.g., noise), as these files were discarded by BCID's default filter.

STATISTICAL ANALYSIS

We conducted separate analyses on the data we collected in 2012 and 2013. For 2012, we compared low Anabat microphones versus low SM2 microphones (i.e., both elevated 2 m). For each phonic group, we tallied the total number of files recorded per night for each detector type from the BCID outputs. We then calculated the mean file count per phonic group per sampling site for each detector. We used generalized estimating equation models, accounting for repeated measures by site, with a negative binomial distribution and log link to test the effects of phonic group, detector type, and their interaction on mean file count per site per detector type (response variable). We conducted a similar analysis for 2013 data, but added height and its corresponding 2-way and 3-way interactions as independent factors. We used least significant differences (LSD) pairwise comparisons to compare responses for significant tests. We used SPSS 20.0.0 (IBM Corporation, Armonk, NY, USA) for all tests and assessed significance at $\alpha = 0.05$.

RESULTS

Due to detector malfunctions, we recorded echolocating bats at 35 sites for 68 detector-nights in 2012. In 2013, we recorded at 33 sites for 61 detector-nights for the low microphones and at 33 sites for 63 detector-nights for the high microphones. Overall, Anabats recorded more bat activity than SM2s; however, the number of detections varied across phonic groups and detector types (Table 1).

In 2012, data acquisition varied by detector type (p = 0.002; Table 2). Anabats recorded more files from all phonic groups combined (mean = 13.72 ± 3.14 files per site) than SM2s (9.05 ± 2.28). When considering data for both Anabats and SM2s combined, we did not record equal amounts of activity by phonic group (p <0.001; Figure 2A). Low phonic group calls were recorded most often, followed by midrange calls, and lastly *Myotis*. However, LSD pairwise comparisons showed that differences were only statistically significant for low versus *Myotis* (p = 0.008) and midrange versus *Myotis* (p = 0.011; Figure 2A). Odds ratios indicated that, relative to *Myotis*, low and midrange phonic group calls were 3.8 times and 2.1 times more likely to be recorded, respectively. The interaction between detector type and phonic group was also significant (p <0.002 Table 2). Anabats recorded more low (mean difference = 22.3 ± 9.9, p = 0.023) and midrange calls (mean difference = 14.3 ± 4.4, p = 0.001) than SM2s, but recorded fewer *Myotis* calls than SM2s (mean difference = -1.8 ± 0.7, p = 0.013; Figure 3A).

In 2013, detector type was not a significant factor in explaining differences in data acquisition (p = 0.754; Table 2). Anabats and SM2s recorded, on average, similar mean file counts per site (7.26 ± 1.24 and 7.03 ± 1.43, respectively). When considering data for both Anabats and SM2s, we did not record equal amounts of activity by phonic groups in 2013 (p <0.001; Figure 2B). As in 2012, low phonic group calls were recorded most often by both detectors, followed by midrange calls, and lastly *Myotis*. Significant differences were observed between each phonic group (Figure 2B). Relative to *Myotis*, the odds of recording low and midrange phonic group calls were 14.7 and 3.6 times greater, respectively; whereas odds of recording low phonic group calls were 2.6 times greater relative to midrange calls. The interaction between detector type and phonic group was also significant (p <0.001; Table 2). Anabats recorded more low (mean difference = 10.7 ± 3.6, p = 0.003) and midrange calls (mean difference = 6.6 ± 1.5, p = <0.001) than SM2s, but recorded fewer *Myotis* calls than SM2s (mean difference = -1.2 ± 0.4, p = 0.004; Figure 3B). Height and its 2-way and 3-way interactions were not significant factors explaining differences in data acquisition (Table 2). When comparing between detector types, Anabats and SM2s performed similarly at both 2 m and 5 m heights (Table 1 and Figure 4).

DISCUSSION

As expected, the omnidirectional SMX-US microphone of the SM2BAT+ and the directional High Mount microphone of the Anabat SD2 recorded different mean file counts per site for all phonic groups. While we did not directly test for the source of this variability, the observed data acquisition differences are likely attributable to a combination of directionality (Waters and Walsch 1994), the interaction between frequency response and directionality (Adams et al. 2012), and weatherproofing (Britzke et al. 2010). Our results suggest that Anabats may record more bat activity overall than SM2s; however, there were significant differences in the ability of both systems to detect particular phonic groups. We did not observe significant differences between detectors deployed at 2 m versus 5 m heights, suggesting that slight differences in detector height may matter less than differences in detector models when designing passive acoustic studies.

Both Anabats and SM2s recorded low phonic groups files most often, followed by midrange, and lastly *Myotis*. Differences in detection rates for these three phonic groups may relate to the capabilities of bat detectors or to disproportionate detectability and species abundance among phonic groups. Low frequency ultrasounds travel farther in air and attenuate less rapidly than high-frequency ultrasounds (Lawrence and Simmons 1982, Parsons 1996, Pettersson 2004). Consequently, when surveying with acoustic bat detectors, we are more likely to detect low phonic group bats versus high-frequency bats like *Myotis* species (Adams et al. 2012). It is possible that differences in the relative abundance of bats in each phonic group may also partially explain the variability among our phonic group data. Low phonic group bats (i.e., primarily *E. fuscus*) are captured most often within our study site, followed by midrange species (i.e., *L. borealis* and *P. subflavus*) and lastly *Myotis* species (O'Keefe et al. 2014). However, we note that there are likely differences in the probability of detecting each phonic group via capture surveys, as we avoided sampling in high clutter areas where *Myotis* bats might be more active (Aldrich and Rautenbach 1987, Owens et al. 2004), and some species may be less susceptible to capture than others (O'Farrell and Gannon 1999).

When Anabats and SM2s are weatherproofed in a manner typical of most long-term passive acoustic monitoring studies, our results suggest that SMX-US microphones detect more *Myotis* bat activity, but less low and midrange phonic group bat activity than Anabats. The omnidirectional SMX-US is capable of recording echolocating bats with flight paths above, below, and behind the microphone. The greater directionality of an Anabat microphone (relative to the SMX-US) limits its ability to sample areas not directly in front of the microphone, and the PVC weatherproofing enclosure likely exacerbates this phenomenon further. Additionally, the foam weatherproofing of the SMX-US is more permeable to sound than the PVC and, thus, the SM2s are likely more exposed to ultrasounds in the environment. A less directional and more exposed microphone, like the SMX-US, should theoretically have a better chance of recording a *Myotis* call (or any bat call) before the call attenuates (Waters and Walsch 1994). This correlates with our finding that SM2s recorded more *Myotis* than Anabats; however, this does not explain why SM2s, on average, recorded fewer low and midrange phonic group files than Anabats. Relative to *Myotis*, low and midrange phonic group calls possess higher source amplitudes, travel farther in air, and are easier to detect with bat detectors at greater distances (Lawrence and Simmons 1982, Corben 2004). The fact that fewer low and midrange bats were recorded by SM2s suggests that Anabat microphones may be more sensitive to these particular frequency ranges, which may allow Anabats to record these “louder” ultrasounds at distances outside the sampling area of SM2s (Waters and Walsch 1994, Limpens and McCracken 2004). In fact, Adams et al. (2012) observed that SM2s had a greater rate of attenuation for low frequency ultrasounds (e.g., 25 kHz) relative to Anabats, which supports the idea that the interaction between frequency response and directionality influences data acquisition. Overall, data acquisition inconsistencies among different detector models are likely attributable to microphone sensitivity, frequency response, and directionality differences (Waters and Walsch 1994, Adams et al. 2012), but weatherproofing strategies may also create variability (Britzke et al. 2010; C. Corben, personal communication 2013), especially in regards to recording specific phonic groups.

We post-processed full-spectrum SM2 data to zero-crossing (ZC) format using WAC2WAV 3.3.0 software in order to match the file parameters of Anabats. This process also allowed the use of BCID, which currently only accepts ZC files. We do not know if post-processing data from one file format to another impacts total file counts. Originally, we intended to conduct a spectral analysis and automatic identification of SM2 data using Sonobat 3.1 NE (SonoBat, Arcata, CA, USA); however, after one season of data collection, we noticed that SM2 calls were burdened with noise and audio distortion in the form of clipping. Sonobat's automated classifier struggled to identify these data and, at times, bat calls were visually indiscernible from noise. We post-processed full-spectrum files to ZC format in WAC2WAV in hopes that BCID could better distinguish bat calls from noise. When testing the "skip noise" feature in WAC2WAV, numerous bat call files were classified as noise. Therefore, we did not implement this feature, but rather relied on the default BCID filter to remove files containing noise. In 2013, we had the option to record directly in ZC format with SM2s, which would have resolved this potential post-processing issue. However, we were instructed by Wildlife Acoustics that SM2s detect more bats in triggered wav mode versus ZC mode, so we continued with our 2012 methods. Overall, we are unsure if using WAC2WAV to convert full-spectrum to ZC format had a negative effect on the total file counts for SM2s.

Our results were contrary to those of D. Solick (personal communication 2012; see Solick et al. 2011) and Adams et al. (2012), as SM2s outperformed Anabats in both of these studies. D. Solick (personal communication 2012) found that a SM2 with a

SMX-US microphone recorded, on average, 20-50 more bat calls per night than an Anabat SD1 utilizing the standard, black microphone without weatherproofing. Adams et al. (2012) found that Anabat SD2s (utilizing High Mount microphones) detected the fewest calls overall (i.e., 5% of emitted signals) in an experiment comparing five different detector models (which included the SM2 with SMX-US microphone). D. Solick (personal communication 2012) surmised that full-spectrum detectors might be better at detecting calls against extraneous noise and have greater detection distances than Anabat SD1s. While it is true that frequency division detectors (e.g., Anabats) only record the sound with the greatest amplitude (Corben 2004), which is often noise, this does not explain why Anabats recorded more bat activity within our study site, an area laden with extraneous noise due to its close proximity to a busy airport and vehicular traffic. Also, it seems unlikely that SMX-US microphones would sample farther than Anabats, as omnidirectional microphones are typically less sensitive than their directional counterparts (Waters and Walsch 1994, Limpens and MacCracken 2004, Adams et al. 2012). Adams et al. (2012) attributed variation in data acquisition to the abilities of specific detectors to detect certain frequency ranges at varying distances from the microphone. These authors found that Anabats did not record any signals >85 kHz in frequency, while SM2s did, and Anabats detected low frequency ultrasounds (e.g., 25 kHz) at greater distances than SM2s. This corresponds with our results, as Anabats tended to record fewer high-frequency *Myotis* calls relative to SM2s, and seemed to have greater detection ranges than SM2s. Contrary to our results, however, Adams et al. (2012) recorded more low frequency calls (e.g., 25 kHz and 55 kHz) with SM2s than

Anabats. Overall, we are uncertain why the total amount of files we detected with Anabats and SM2s contrasted with that of Solick et al. (2011) and Adams et al. (2012). It seems likely that differences in methodology (i.e., the use of weatherproofing [Britzke et al. 2010], deployment height/microphone orientation [Weller and Zabel 2002], gain/trigger settings [D. Solick, personal communication 2012, Adams et al. 2012], data post-processing, the use of artificial ultrasonic calls [Adams et al. 2012]) and the environment in which sampling was conducted are likely responsible (Parsons 1996). Making comparisons across studies that occur in different field settings is challenging, as the rate at which sound attenuates, and thus the sampling area, will vary due to differences in climate and vegetation (Parsons 1996, C. Corben, personal communication 2014). Furthermore, local bat fauna and activity rates may be dissimilar.

Height (2 m vs. 5 m) did not affect the total number of bat files recorded by either SM2s or Anabats. We expected microphones elevated at greater heights above the understory vegetation would record significantly more bat activity (Weller and Zabel 2002); however, mean file counts per site were similar for both detector types. We expected high SM2s to outperform low SM2s, as many of the calls collected in 2012 with 2 m microphones were laden with noise, perhaps due to close proximity to understory vegetation. However, 2 m and 5 m SM2 microphones performed similarly in 2013, suggesting that these microphones either had overlapping sampling areas or they are just inherently sensitive to environmental noise. Anabats at 2 m and 5 m heights also performed similarly, which further suggests that a distance of 3 m between microphones may be insubstantial for discerning differences in bat activity due to overlapping sampling areas.

Overall, data acquisition among different commercially available bat detectors is highly variable (Waters and Walsh 1994, Parsons 1996, Solick et al. 2011, Adams et al. 2012); yet, different models will continue to be used, often interchangeably, in bat research across the globe. Therefore, if we want to better portray reality with acoustic sampling efforts, it is imperative that further comparative studies be conducted to determine how different models perform relative to one another. With any new bat detector technology, the capabilities and limitations of the equipment must be addressed (Adams et al. 2012), and with any scientific methodology, it is crucial to develop a standardized approach. In regards to acoustic sampling, standards must be set for weatherproofing systems, hardware/software settings, and deployment techniques, if possible. While it is unlikely that any single methodology will universally satisfy the research or management goals of all acoustic studies (Adams et al. 2012), minimizing variation to any degree with undoubtedly be beneficial. Therefore, as recommended by Adams et al. (2012), we too encourage authors to present detailed information about their methodologies, especially technical hardware/software settings used with bat detectors.

IMPLICATIONS

Without a complete understanding of the capabilities and limitations of modern bat detectors, studies designed to assess bat activity may yield inaccurate estimates and may under-sample some phonic groups or bat species. It is likely that passive acoustic sampling will continue to play larger roles in future bat monitoring efforts, so decisions about acoustic equipment and deployment could have significant effects on species management. For instance, the US Fish and Wildlife Service has recently implemented major changes to the summer survey protocol for the federally endangered Indiana bat (USFWS 2014) by requiring passive acoustic sampling using only directional microphones (e.g., the Anabat, among other models). In this case, the stock SMX-US omnidirectional microphone could not be used, even though our results suggest this microphone detects more *Myotis* bat activity than directional Anabat microphones housed in PVC. On the other hand, Anabats may be better suited for bat monitoring efforts at wind energy facilities, where the detection of low and midrange phonic group bats (e.g., *L. noctivagans*, *L. cinereus*, and *L. borealis*) is essential. These species comprise the bulk of wind energy-related fatalities in the eastern United States (Kunz et al. 2007), and proper site planning and mitigation efforts rely on accurate activity estimates for these species during both pre- and post-construction acoustic surveys. These are merely two examples, but we must make every effort to understand and reduce our sampling biases when studying small, volant, nocturnal mammals. Additional comparative studies will continue to inform best practices for bat studies, which will ultimately aid in the management and conservation of these valuable wildlife species.

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TABLES

Table 1. Total number of identifiable bat files and mean (± S.E.) bat files recorded by phonic group for Anabat SD2 and SM2BAT+ acoustic detectors deployed at sites near the Indianapolis International Airport in central Indiana, May-August 2012 and 2013. Anabat and SM2 data are presented for low and high microphone elevations.

					Total Bat Files Recorded			Mean Bat Files Recorded (± S.E.)		
					Phonic Group			Phonic Group		
Year	Detector	Mic Height	# Sites Sampled	# Nights Sampled	Low	Mid	*Myotis*	Low	Mid	*Myotis*
2012	Anabat	Low (2 m)	35	68	1812	1606	164	39.8 ± 12.1	23.7 ± 7.2	2.7 ± 0.7
	SM2		35	68	771	619	263	17.5 ± 7.7	9.3 ± 3.0	4.5 ± 1.2
2013	Anabat	Low (2 m)	33	61	2337	1012	46	35.8 ± 10.2	14.1 ± 3.8	0.8 ± 0.2
	SM2		33	61	1288	636	152	20.1 ± 7.1	8.7 ± 3.7	2.4 ± 0.8
	Anabat	High (5 m)	33	63	2111	965	39	31.4 ± 7.9	13.9 ± 2.8	0.8 ± 0.2
	SM2		33	63	1622	444	93	26.0 ± 9.4	6.3 ± 1.7	1.8 ± 0.4

Table 2. Significance tests for generalized estimating equation models for differences in data acquisition during a study near the Indianapolis International Airport in central Indiana, May-August 2012 and 2013.

	2012 (2 m mics; 35 sites)			2013 (2 m & 5 m mics; 33 sites)		
Effect	df	Wald Chi-Square	p	df	Wald Chi-Square	p
Detector type	1	9.326	0.002	1	0.098	0.754
Phonic group	2	29.144	<0.001	2	75.898	<0.001
Detector type x Phonic group	2	76.725	<0.002	2	28.216	<0.001
Height	-	-	-	1	0.375	0.540
Height x Detector type	-	-	-	1	0.186	0.666
Height x Phonic group	-	-	-	2	2.594	0.273
Height x Phonic group x Detector type	-	-	-	2	3.393	0.183

FIGURES

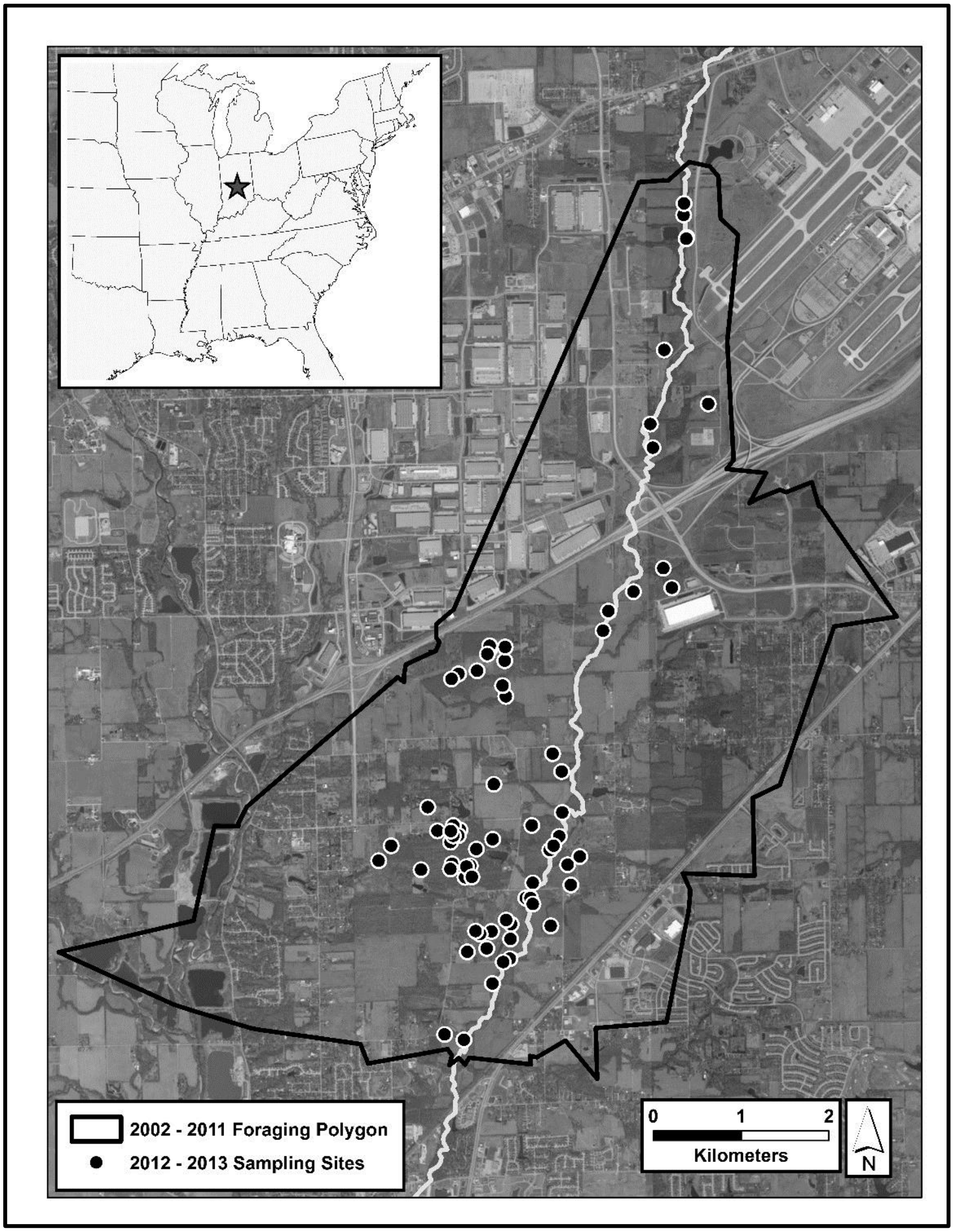

Figure 1. Location of 71 acoustic sampling points (black dots) near a riparian corridor west of Indianapolis International Airport in central Indiana surveyed from May-August 2012 and 2013. The black polygon delineates the potential foraging area for Indiana bats (*Myotis sodalis*), which was derived from combined foraging telemetry data from 2002-2011.

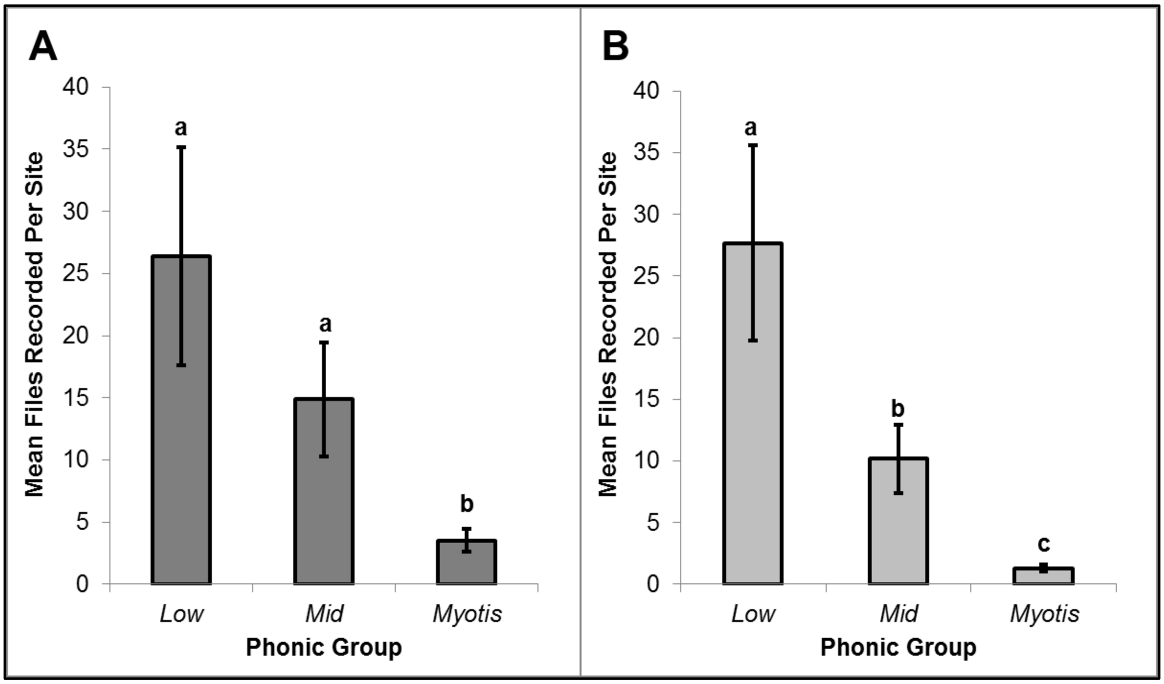

Figure 2. Mean bat call files recorded per phonic group in 2012 (A) and 2013 (B) for Anabat SD2 and SM2BAT+ acoustic detectors deployed at sites near the Indianapolis International Airport in central Indiana. Anabat and SM2 data are combined for each year. Means that were significantly different ($p < 0.05$) in least significant differences pairwise comparisons are denoted by different letters above the standard error bars.

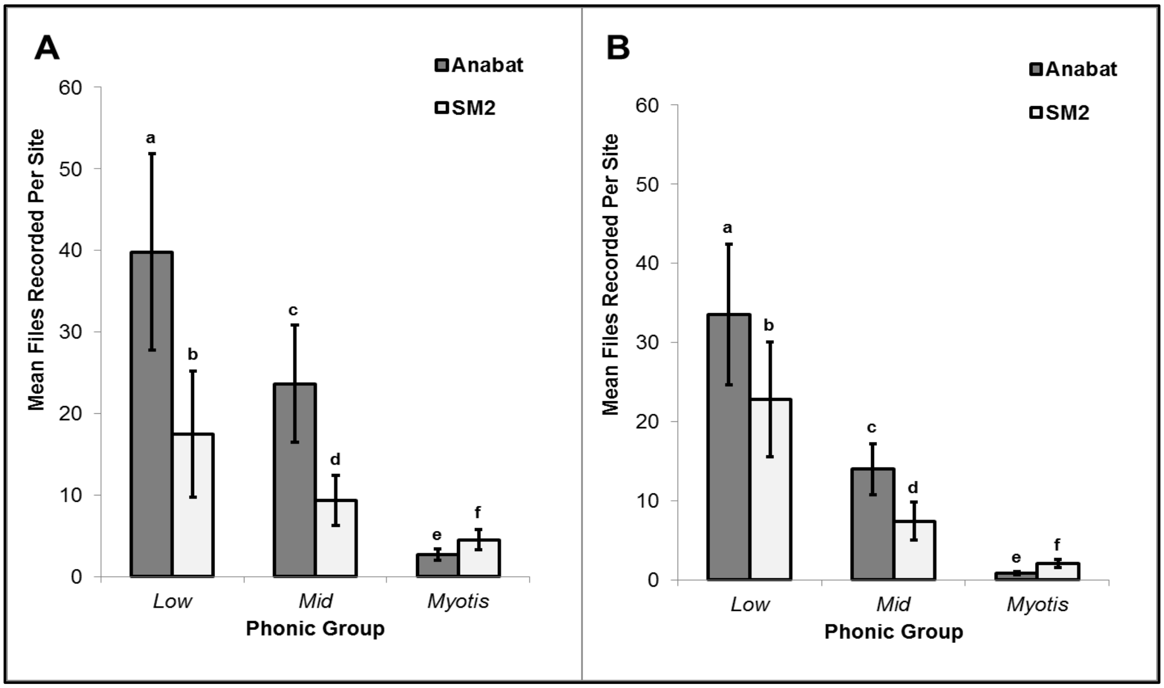

Figure 3. Mean bat call files recorded per phonic group per site in 2012 (A) and 2013 (B) for Anabat SD2 and SM2BAT+ acoustic detectors deployed at sites near the Indianapolis International Airport in central Indiana. Means that were significantly different ($p < 0.05$) in least significant differences pairwise comparisons are denoted by different letters above the standard error bars.

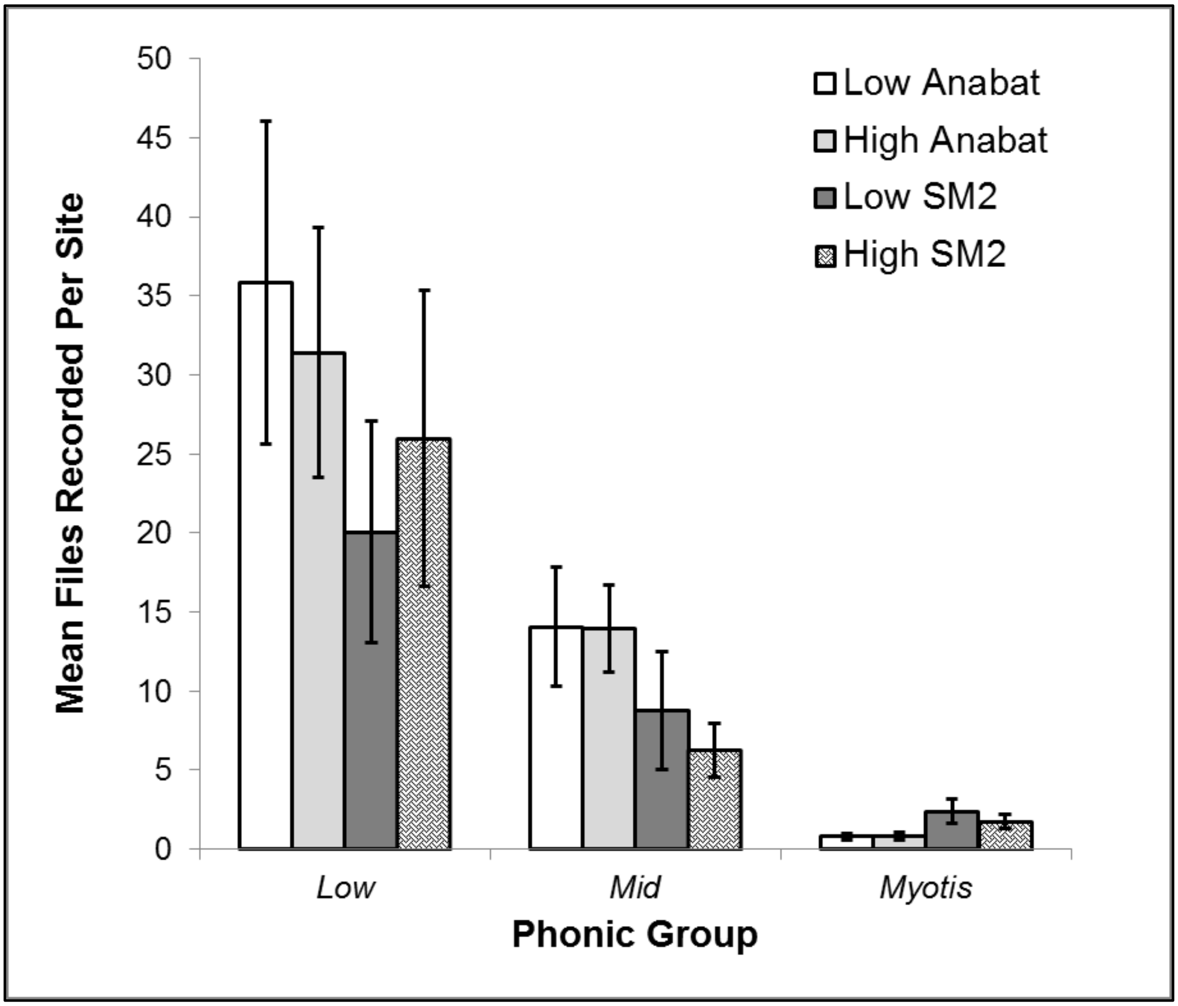

Figure 4. Mean bat call files recorded per phonic group by detector height for Anabat SD2 and SM2BAT+ acoustic detectors deployed at sites near the Indianapolis International Airport in central Indiana, May-August 2013. No significant differences were observed between detector height and its 2-way and 3-way interactions with detector type and phonic group.

CHAPTER 2

FACTORS AFFECTING THE PROBABILITY OF ACOUSTIC DETECTION AND SITE OCCUPANCY OF INDIANA BATS (*MYOTIS SODALIS*) NEAR A KNOWN MATERNITY COLONY

INTRODUCTION

The federally endangered Indiana bat (*Myotis sodalis*) is an insectivorous, forest-dwelling mammal found throughout much of the eastern United States. Current populations face numerous threats, including habitat loss and alteration (Richter et al. 1993, Menzel et al. 2001, Sparks et al. 2005), pesticide use (Schmidt et al. 2001), disturbance of hibernacula by humans (Johnson et al. 1998), and the emergent white-nose syndrome fungal disease (Thogmartin et al. 2013). Yet, some uncertainty remains about the specific habitat requirements for this species (Callahan et al. 1997, Menzel et al. 2005), mostly because these small mammals are rarely conspicuous in the environment and their presence or absence cannot be determined with absolute certainty. Indiana bats are a highly-mobile, nocturnal species capable of exploiting ephemeral resources in structurally-complex, interior forests (Murray and Kurta 2002, Menzel et al. 2005). These areas are difficult to sample using acoustic bat detectors or mist-nets and, even in forests that harbor known Indiana bat populations, documenting presence remains a challenge (Robbins et al. 2008).

Beginning in the 1980s, the advent and application of radio-transmitters suitable for small vespertilionid bats allowed for rapid increases in our knowledge of Indiana bat summer ecology (Callahan et al. 1997, Gardner and Cook 2002, Carter 2006). With radio telemetry, researchers discovered numerous maternity colonies across the species' range and, currently, the bulk of known colonies occur in the Midwestern United States (Gardner and Cook 2002, Kurta et al. 2002, Menzel et al. 2005). Although radio telemetry provides many benefits, its intense labor demands often prevent the collection of samples adequate for making robust conclusions over large spatial scales (Callahan et al. 1997, Clement and Castleberry 2012). Consequently, information gaps still remain for many forest-dwelling bats in the Midwestern United States (Miller et al. 2003, Ford et al. 2005, Whitaker and Sparks 2008). The recent coupling of acoustic bat detectors and occupancy modeling techniques (e.g., Duchamp et al. 2006, Yates and Muzika 2006, Gorresen et al. 2008) now provides an alternative by which to gain additional insight into bat ecology. Automated bat detectors allow researchers to sample large landscapes for lengthy time periods (Murray et al. 1999, Miller 2001) and often provide higher detection rates than capture methods alone (Murray et al. 1999, O'Farrell and Gannon 1999). Furthermore, pairing data from bat detectors with modeling techniques allows for activity and site occupancy estimates to be generated across large spatial scales (Ford et al. 2005, Yates and Muzika 2006). While acoustic sampling has promise in this regard, this technique also has limitations such as accounting for varying detection probabilities (Hayes 2000, Duchamp et al. 2006, Yates and Muzika 2006).

Acoustic sampling with ultrasonic bat detectors has unavoidable biases (Murray et al. 1999, O’Farrell and Gannon 1999, Hayes 2000, Corben and Fellers 2001). For example, bat detectors sample finite airspaces and only echolocating bats passing near the detector will be recorded (Weller and Zabel 2002, Limpens and McCracken 2004). In turn, silent or distant individuals go undetected and, therefore, detectability will be imperfect (or <1) and fluctuate over time (MacKenzie et al. 2002, Yates and Muzika 2006). The probability of recording an individual given that it is present (henceforth, “detectability”), is dictated by the sampling area of the bat detector’s microphone (Downes 1982, Waters and Walsch 1994, Limpens and McCracken 2004), the amplitude and frequency of emitted bat calls (Lawrence and Simmons 1982, Parsons 1996, Adams et al. 2012), and environmental (Schnitlzer and Kalko 2001, Broders et al. 2004) and atmospheric conditions of the site being sampled (Griffin 1971, Limpens and McCracken 2004). Detection rates are typically lower with higher levels of clutter (Broders et al. 2004), environmental noise (Weller and Zabel 2002), relative humidity (Lawrence and Simmons 1982), echolocation frequency (Adams et al. 2012), and distance of the sound source from the detector’s microphone (Corben and Fellers 2001).

The probability that a foraging site will be occupied is affected by extrinsic factors that impact bat behavior, including seasonality (Walsh and Harris 1996, Robbins et al. 2008), time of night (Kunz 1973, Anthony et al. 1981), anthropogenic disturbance (Schaub et al. 2008, Stone et al. 2009, Bennett and Zurcher 2012, Berthinussen and Altringham 2012), predation risk (Speakman 1995, Lima and O’Keefe 2013, Thomas and Jacobs 2013), prey availability (Anthony et al. 1981, Barclay 1991, Kusch et al. 2004), and weather conditions (Anthony et al. 1981, Parsons et al. 2003, Burles et al. 2009). Site occupancy by bats may also be influenced by site-specific characteristics, including the presence of edge habitat (Murray and Kurta 2004, Morris et al. 2010), roost structures (Clement and Castleberry 2012), and water resources (Furlonger et al. 1987, Seidman and Zabel 2001). Indiana bat maternity colonies generally occupy habitats in close proximity to water (Murray and Kurta 2002, Ford et al. 2005, Menzel et al. 2005, Sparks et al. 2005, Carter 2006) that contain roost trees with large diameters, high amounts of solar exposure, and exfoliated bark (Callahan et al. 1997, Kurta et al. 2002, Carter 2006). Within our study site, Indiana bats forage in a variety of land-cover types, ranging from deciduous forests and riparian areas to agricultural fields and wetlands (Sparks et al. 2005, O'Keefe et al. 2014*b*).

Occupancy modeling allows researchers to pair presence/absence data for a target species with covariates to gain information about detection probabilities, site usage, and activity trends over time (Yates and Muzika 2006, Gorresen et al. 2008). In general, bat activity is known to be highly variable and can differ substantially between nights (Hayes 1997); therefore, detecting a target species with acoustics is not assured even if presence was recently documented. Conducting repetitive presence-absence surveys is one method by which to counter false absences and estimate detection probabilities with greater accuracy (MacKenzie and Royle 2005). Furthermore, sampling more sites reduces detection biases for rare species (MacKenzie and Royle 2005) and including detection probabilities in the overall occupancy models enhances the accuracy of site occupancy estimates (MacKenzie et al. 2002).

Yates and Muzika (2006) used data from automated bat detectors to assess the effects of various local and landscape-scale habitat characteristics on detection and occupancy probabilities for Indiana bats and determined that density of large diameter snags positively affected occupancy rates for this species. Likewise, we aimed to create detection-adjusted occupancy estimates for Indiana bats in an effort to determine what factors influence detectability and occupancy within our study area. We conducted acoustic sampling near an active Indiana bat maternity colony and its numerous primary and alternate roosts (Whitaker et al. 2011). This colony has persisted for at least 18 years in a highly-modified area that borders the city of Indianapolis, Indiana (Whitaker and Sparks 2008). Suburban and urban sprawl is commonplace and the green space used by the maternity colony is confined by several multiple-lane highways, including Interstate 70 (I-70; Sparks et al. 1998, Whitaker and Sparks 2008). The persistence of this colony in a relatively small study site, as well as prior knowledge of maternity roost locations (Whitaker et al. 2011), gave us a unique opportunity to pinpoint habitat features that influence detectability and site occupancy for Indiana bats in a rural-urban interface.

We investigated the effects of vegetative clutter, weather conditions, and the date of sampling on the probability of detecting Indiana bats. Overall, we expected the detectability of Indiana bats to be negatively related to vegetative clutter (Weller and Zabel 2002, Broders et al. 2004, Schaub et al. 2008), relative humidity (Griffin 1971, Lawrence and Simmons 1982), and wind speeds (Eckert 1982). Conversely, we expected detectability to be positively related to temperature and date of sampling, as bat activity is typically greater on warmer nights (Erickson and West 2002), especially later in the summer when juveniles are capable of flight (Anthony et al. 1981, Whitaker and Sparks 2008). We also investigated how proximity to site-specific landscape features and habitat types influenced Indiana bat site occupancy. We expected Indiana bats would more often occupy sites closer to popular maternity roosts, as lactating females would be actively coming and going from roosts due to foraging and nursing obligations (Clark et al. 2002, Murray and Kurta 2004). We also expected that occupancy would be higher in land-cover types suitable for foraging (i.e., forests or hydric habitats; Carter 2006) or near roosts. We expected that proximity to edges between cover types would have little impact on occupancy, as Indiana bats in the Midwest are believed to be behaviorally adapted to fragmented landscapes (Brack and Whitaker 2006) and capable of foraging in a variety of habitats (Sparks et al. 2005). Lastly, we expected that Indiana bats would avoid human disturbance and, thus, occupancy would be lower near paved roads (Schaub et al. 2008, Stone et al. 2009, Bennett and Zurcher 2012).

STUDY AREA

This study was conducted on 1,045 ha of property west-southwest of the Indianapolis International Airport between the cities of Mooresville and Plainfield, Indiana (Figure 1). The East Fork of White Lick Creek, an 84 km long perennial stream, flows north-south through the study site (Stahl et al. 1997, Whitaker et al. 2004). I-70, running northeast-southwest, splits the study site into “northern” and “southern” sections, with State Road 67 forming the eastern and southern borders, and State Road 267 forming the western border (Figure 1). The study site north of I-70 is limited to a narrow band of riparian forest, as the surrounding landscape is heavily developed with airport runways and busy highways to the east, a warehouse district to the west, residential subdivisions to the north, and large electrical substations and accompanying power lines to the south. Anthropogenic activity is commonplace and commercial planes fly within a few hundred meters of the canopy throughout the night. The study site south of I-70 has been heavily modified by human activities and consists of numerous, fragmented land-cover types, including agricultural lands, wetlands, pasture/grasslands, residential/commercial developments, forested riparian corridors, and remnant deciduous forests. Several parcels of land have been permanently set aside as forested wildlife refuges, replanted wetlands or forests (Sparks et al. 2009), or local parks for public recreation. Since 1992, the Indianapolis Airport Authority has created 54.5 ha of wetlands within the study site and reforested 323 ha with ~560,000 native tree seedlings (Sparks et al. 2009, O'Keefe et al. 2012). Dominant overstory tree species include American sycamore (*Platanus occidentalis*), shagbark hickory (*Carya ovata*), common hackberry (*Celtis occidentalis*), eastern cottonwood (*Populus deltoides*), white oak (*Quercus alba*), red oak (*Q. rubra*), Ohio buckeye (*Aesculus glabra*), box elder (*Acer negundo*), black walnut (*Juglans nigra*), and various ash (*Fraxinus*) and maple (*Acer*) species. Asian bush honeysuckle (*Lonicera maackii*), a non-native invasive species, has overrun areas within the study site, predominantly the banks of the East Fork of White Lick Creek and interiors of disturbed forests.

Since 1996, the study site has been home to a long-term study of the summer foraging and roosting ecology of the federally endangered Indiana bat (Whitaker et al. 2004, O'Keefe et al. 2014*b*). From 1997-2013, nine bat species have been captured in mist-nets in the study site, including big brown bats (*Eptesicus fuscus*), silver-haired bats (*Lasionycteris noctivagans*), hoary bats (*Lasiurus cinereus*), eastern red bats (*Lasiurus borealis*), evening bats (*Nycticeius humeralis*), tri-colored bats (*Perimyotis subflavus*), northern long-eared bats (*M. septentrionalis*), little brown bats (*M. lucifugus*), and Indiana bats (Whitaker et al. 2004, O'Keefe et al. 2014*b*).

In 2012, mean minimum and maximum nightly temperatures for May were 14.9 and 24.0°C, respectively; for June, 16.0 and 26.3°C; for July, 23.1 and 31.4°C; and August, 18.9 and 28.9°C. In 2013, mean minimum and maximum nightly temperatures for May were 15.2 and 21.9°C, respectively; for June, 18.0 and 24.8°C; for July, 18.8 and 25.6°C; and August, 22.5 and 26.1°C. Temperature data were measured at the Indianapolis International Airport weather station 4 km northeast of the study area center and downloaded from the National Climatic Data Center (http://www.ncdc.noaa.gov).

METHODS

SITE SELECTION

We combined 95% minimum convex polygons, derived from foraging telemetry data collected for Indiana bats in previous years (2002-2011; Whitaker et al. unpublished data), to create a single polygon in ArcMap 10.0 (ESRI, Inc. Redlands, CA, USA) that outlined potential Indiana bat foraging habitat within our study site (Figure 1). From 16 May to 6 August 2012 and 15 May to 7 August 2013, we deployed bat detectors to sample 71 random points within this polygon. We sampled in a variety of land-cover types, including wetland/riparian areas, deciduous forests, pasture/grasslands, replanted forests (<20 years old), and agricultural lands. Our sampling effort was restricted because private property and human activity was so commonplace within the study site. Therefore, we were forced to replace random points that were inaccessible (e.g., private property) or in locations where bat detector equipment was in jeopardy of being stolen/tampered with (e.g., public parks) or damaged (e.g., active cow pastures). Subsequently, we did not sample land-cover types in proportion to their availability on the landscape.

On average, acoustic sampling occurred 2.17 ± 0.25 km (range 0.20-8.39 km) from Indiana bat primary maternity colony roosts. As part of a long-term inventory and monitoring effort, we also mist-netted 12 semi-permanent net sites for a total of 78 net-nights in 2012 (O'Keefe et al. 2012) and 77 net-nights in 2013 (O'Keefe et al. 2014*b*). Ten net sites occurred along the East Fork of White Lick Creek and two occurred within a nearby forested area (~1 km from the creek). On average, mist-net sites were 3.58 ± 0.92 km (range 0.39-9.08 km) from Indiana bat primary maternity colony roosts. We radio-tagged adult and juvenile Indiana bats, tracked tagged individuals to day roosts, and estimated nightly foraging locations using multi-azimuth triangulations (e.g., O'Keefe et al. 2014*b*). We conducted emergence counts/spotlight checks, as feasible, in effort to estimate population size and intensity of roost use. See O'Keefe et al. (2012, 2014*b*) for more details about capture, tracking, and emergence count methods.

DETECTOR SETUP

In 2012, we sampled 35 sites for a total of 70 nights and, in 2013, we sampled 36 sites for a total of 72 nights. At each sampling point, we recorded bat calls with Wildlife Acoustic omnidirectional SMX-US microphones attached to SM2BAT+ bat detectors (henceforth, “SM2”; Wildlife Acoustics, Inc., Concord, MA, USA). The microphones were connected to the detectors with 10 m cables and elevated 2 m on a metal pole (Weller and Zabel 2002). We used the stock, foam shielding to weatherproof SMX-US microphones. We programmed SM2s to record monaural, full-spectrum data with a bit depth of 16, a sampling rate of 384,000 kHz, and a WAC0 audio compression. The following settings were used with SM2s, trigger: trig left = 18db, trig win left = 2.0 s; gain: 48db, left microphone = +0.0db; high-pass filter: HPF left = fs/24; and low-pass filter: LPF left = OFF. Sampling occurred from pre-dusk (20:00 EDT) until post-dawn (8:00 EDT) each night for two consecutive detector-nights at each sampling point. A detector-night was defined as one uninterrupted night of recording. Data were included in our analyses only if a full detector-night of sampling was achieved, and in 2012, we discarded two nights due to detector malfunctions. To record the best calls possible, we selected a point with the least amount of clutter ≤ 25 m from the random sampling point and oriented microphones towards potential bat flyways (Larson and Hayes 2000).

HABITAT SAMPLING

For each sampling point, we delineated a circular vegetation plot (0.07 ha; 15 m radius) centered on the microphone (Weller and Zabel 2002). Within this plot, we delineated a nested circular plot (0.02 ha) with radii extending 7.5 m in the four cardinal directions. We estimated canopy and mid-story closure, counted the number of saplings <10 cm in diameter in the nested plot, and measured the diameter at breast height (DBH) of all trees/snags ≥10 cm in the full plot. We defined the mid-story as trees with heights ranging from ~2-10 m and the canopy as trees with heights >10 m. Canopy and mid-story closure were visually estimated by the primary author as low (0-25%), moderate (26-50%), high (51-75%), or very high (76-100%); five visual estimates were made for each plot (one directly above the microphone, and one in the center of each of the four quadrants). We averaged canopy and mid-story closure estimates for each sampling point.

We downloaded wetland and riparian spatial data from the National Wetlands Inventory database (http://www.fws.gov/wetlands/Data/State-Downloads.html). We calculated distances from each sampling point to the nearest wetland/riparian area using the Spatial Join tool in ArcMap 10.0. We calculated distances from each sampling point to the nearest paved road, habitat edge, water source, and habitat type using 2012 Bing aerial maps and the Measure tool in ArcMap 10.0. We calculated distances to maternity roost locations using GPS coordinates obtained from homing telemetry efforts from previous years and in 2012 and 2013 (Whitaker et al. 2011, O'Keefe et al. 2012, 2014*b*). Roost switching occurred regularly (O'Keefe et al. 2012, 2014*b*); thus, we defined the primary maternity colony roost as the tree or bat box that housed the largest proportion of Indiana bats (based on emergence count and homing telemetry data) for each detector-night. If there was no emergence count data for a particular night of acoustic sampling, we used the most recent count data relative to our sampling date. We obtained hourly humidity and wind speed data from the National Climatic Data Center (http://www.ncdc.noaa.gov) and hourly temperature data from the internal sensors of each SM2.

ECHOLOCATION DATA ANALYSIS

We used WAC2WAV 3.3.0 software (Wildlife Acoustics, Inc., Concord, MA, USA) to convert SM2 full-spectrum data to zero-crossing format with the following parameters: division ratio = 8, maximum file duration = 15 s, and minimum time between calls = 2 s. The SMX-US to UT filter was applied in WAC2WAV 3.3.0 to achieve a flatter frequency response, as suggested by Wildlife Acoustics (personal communication 2012). We used Bat Call ID 2.5b (henceforth, "BCID"; Bat Call Identification, Inc., Kansas City, MO, USA) automated software to identify bat call files to species (Romeling et al. 2012). The software referred to an internal reference call library for bats that occur in Indiana (1,546 calls of nine species), required a pulse count of ≥5 for file identification, and reported ≥70% species confidence level. BCID identified files to species based on a clustering algorithm and call parameters such as duration, minimum frequency, slope at the flattest portion of the call, and frequency at the knee of the call (R. Allen, personal communication 2014). The BCID analyses considered only *E. fuscus*, *L. noctivagans*, *L. cinereus*, *L. borealis*, *N. humeralis*, *P. subflavus*, *M. septentrionalis*, *M. lucifugus*, and *M. sodalis*. We programmed BCID to ignore *M. leibii* and *M. grisescens* because these two species have not been captured in mist-nets within our study site over the past 15 years (Whitaker et al. 2006, O'Keefe et al. unpublished data); this procedure also simplified *Myotis* species identification by reducing potential misidentifications. Identification of *Myotis* echolocation calls in the eastern United States is not foolproof (Britzke 2013); therefore, to remain conservative and avoid misidentifications, all files identified as Indiana bats by BCID were confirmed manually in AnalookW 3.8y (Corben, www.hoarybat.com) by comparing quantitative measures of recorded call files to a reference call library and a dichotomous key for identifying echolocating bats in the eastern U.S. (S. Amelon, personal communication 2012, Ford et al. 2005).

MODELING METHODS

We selected covariates to be used in our models based on published literature, grouping variables into one of six categories: atmospheric attenuation, clutter, temporal, microhabitat, distance to landscape feature, and distance to land-cover types (Table 1). Using SPSS 20.0.0 (IBM Corporation, Armonk, NY, USA), we ran a Pearson's correlation and retained uncorrelated distance to landscape feature covariates (Pearson $r^2 < 0.25$; Clement and Castleberry 2012). We ran a principal component analysis (Miracle 1974) and parallel analysis (Horn 1965) to reduce the number of clutter covariates to be entered into the detection and occupancy models. The covariate entitled "forest closure" was derived from the principal component analysis and contained mean canopy closure, mean mid-story closure, and number of trees ≥10 cm DBH in the vegetation plot.

We used an information theoretic approach and single-season occupancy models (Royle and Nichols 2003) in Presence 6.1 software (Hines 2006) to evaluate candidate probability of detection and site occupancy models. Each two-night detector deployment was split into two sampling visits, with one detector-night equaling one visit. A site was considered occupied if one recorded call file was identified as an Indiana bat during a single night of sampling (Yates and Muzika 2006). We pooled presence-absence data from 2012 and 2013 without testing for differences between years. The Indiana bat maternity colony has foraged consistently in the same area for >10 years (Whitaker et al.

unpublished data, O’Keefe et al. unpublished data). Because we sampled within an area defined by combined foraging telemetry data from 2002-2011 (Whitaker et al. unpublished data; Figure 1), we did not expect that Indiana bats would use the study site differently between years. Using existing literature and field observations, we created *a priori* models (Appendices 1-2) to assess the probability of detection and site occupancy for Indiana bats in relation to selected covariates (Table 1).

We created 15 *a priori* models to address the probability of detection (p) for Indiana bats (Appendix 1). Models contained varying combinations of temporal, weather, and clutter covariates (Table 1; Appendix 1). We created 18 *a priori* models for site occupancy (ψ) that contained varying combinations of clutter, microhabitat, distance to landscape feature, and distance to habitat type covariates (Table 1; Appendix 2). We standardized all covariate data with the “normalize covariate” option in Presence 6.1, which subtracted the mean and divided by the standard deviation for each covariate.

We used Akaike’s Information Criterion score adjusted for small sample sizes (AIC_c) to identify the best models for p and ψ. The models with the lowest AIC_c scores and fewest parameters were considered to have the best fit (Burnham and Anderson 2002). We used AIC_c scores, the model differences (ΔAIC_c) from the model with the lowest AIC_c, and Akaike model weights to evaluate the relative strengths of each model (Burnham and Anderson 2002). We identified the confidence set as all models with weights within 10% of the AIC weight for the top model (Hein et al. 2008). For each covariate appearing in the confidence models, we model-averaged parameter estimates and standard errors across all models in the confidence set in which the covariate appeared (Burnham and Anderson 2002). We considered covariates to be significant if their 85% confidence interval excluded zero (Arnold 2010). We included significant covariates for p in the larger occupancy models (MacKenzie et al. 2002). We then model-averaged the ψ model set so as to overcome uncertainty and reduce bias (Burnham and Anderson 2002), and reported significance with an 85% confidence interval (Arnold 2010). We used parametric boot-strapping with 1,000 permutations in Presence 6.1 to evaluate the goodness-of-fit for the ψ models with the most parameters (MacKenzie and Bailey 2004). Lastly, we calculated odds ratios for all statistically significant p and ψ covariates (Hosmer and Lemeshow 2000, Yates and Muzika 2006).

RESULTS

In 2012, we recorded 2,774 files, of which 1,461 were identified to species by BCID. In 2013, we recorded 3,903 files, of which 1,660 were identified to species. All nine species known to occur within our study site were identified from passive acoustic samples. Only 4.4% of the total identifiable bat files recorded were classified as Indiana bats by BCID. Indiana bats were detected at 43.7% (i.e., 31 of 71) of sampled sites and on 32.1% (i.e., 45 of 140) of detector-nights. The naïve probability of detection was 0.41 in 2012 and 0.21 in 2013. Indiana bats were detected on more occasions and at more sampling points in 2012 (86 files; 21 sampling points) than in 2013 (50 files; 10 sampling points). Nearly 82% of detections (18 points in 2012 and 9 points in 2013) were from sites south of I-70. Our sampling effort per month was not proportional, but when looking at months we sampled more completely (e.g., May-July), Indiana bat detections were more common in July (Table 3). This roughly corresponds with the onset of juvenile volancy within our study site, which was first observed (via captured juveniles) on 2 July 2012 and 17 July 2013 (O'Keefe et al. 2012, 2014*b*). Detections were most common in wetland/riparian areas, deciduous forests, and pasture/grassland land-cover types, and less common in agricultural lands; however, we did not sample land-cover types in proportion to their availability (Table 2). It should be noted that Indiana bats were detected in all land-cover types sampled within our study site, and the total number of detections per land-cover type was positively related to sampling effort (not tested; Table 2).

Four probability of detection models appeared in the confidence set; the mean probability of detection was 0.56 for these models, the combination of which carried 84.6% of the total AIC_c model weight (Table 4). The top model, "Forest Attenuation," included forest closure, mean nightly temperature, and mean nightly humidity and accounted for 57% of the total model weights (Table 4; Appendix 1). The global model was the second best model, followed by "Forest Structure", which included forest closure and number of saplings. "Forest Phenology," which ranked last in the confidence set, contained both forest closure and date of sampling and carried only 5.8% of the AIC_c model weight (Table 4; Appendix 1). Forest closure and mean nightly temperature were the only covariates with model-averaged 85% confidence intervals that did not overlap zero (Table 5). Forest closure occurred in all top models, while mean nightly temperature occurred in half (Table 4); both had statistically significant positive relationships with probability of detection (forest closure odds ratio = 2.93, mean nightly temperature odds ratio = 3.29; Table 5; Figures 2 and 3). Estimates of other variables were not informative, as model-averaged confidence intervals included zero (Table 5).

All 18 candidate occupancy models appeared in the confidence set (Table 6). The null model was the top-ranked model (Table 6), indicating that none of the *a priori* models better explained Indiana bat occupancy. The global model for occupancy would not converge, suggesting we lacked sufficient detections relative to the number of predictor variables we were testing (J. Hines personal communication 2013). The naïve estimate of the probability of occupancy was 0.42 for the null model. ΔAIC_c was < 2 for eight other competing models (Table 6); however, goodness-of-fit tests suggested that the candidate models were not well-fitted ($\hat{c} < 0.5$). Thus, the null model was likely of best fit simply because it was the most parsimonious (Table 6). The confidence set of occupancy models included covariates from all possible categories (Tables 1 and 6), but with the exception of distance to agriculture, none of the covariates were statistically significant, as each had 85% confidence intervals that overlapped zero (Table 7). Distance to agriculture had a significant negative effect on site occupancy for Indiana bats (odds ratio = 0.63; Table 7; Figure 4).

DISCUSSION

The federally endangered Indiana bat is difficult to detect with traditional sampling methods (Robbins et al. 2008). For example, Romeling et al. (2012) showed that at least 28 days of continuous passive acoustic sampling is required to document presence with 95% confidence. Our results suggest that even when sampling in a relatively confined study site in close proximity to the primary roosts of a large maternity colony (e.g., ≥150 individuals by mid-July), the probability of detecting Indiana bats with automated bat detectors remains relatively low (i.e., only 0.56). Forest characteristics (e.g., canopy closure, mid-story closure, and number of trees within the acoustic sampling radius) and mean nightly temperatures significantly influenced detection probabilities. However, only distance to agriculture had a significant effect on Indiana bat occupancy within our study site. We suspect that we failed to find many factors to explain occupancy due to low power in our models, which were based on only a few total Indiana bat detections.

In 2012-2013, fewer than 5% of recorded bat files were identified as Indiana bats, and this species was detected on less than one third of sampled nights. We suspect this is an underestimate of Indiana bat activity and that limitations associated with passive acoustic detectors are likely responsible for our low detection rates. Bat detectors sample limited areas (Limpens and McCracken 2004), and only a portion of bat activity is recorded each night, potentially < 25% (Adams et al. 2012). Furthermore, detection probabilities are not equal among all bat species, as some species use calls with greater intensities or signal types that are more conspicuous to bat detectors (Broders et al. 2004, Limpens and McCracken 2004). Broadband, high-frequency calls, like those used by Indiana bats, attenuate rapidly (Schnitlzer and Kalko 2001, Limpens and McCracken 2004) and, therefore, are difficult to detect.

Low detection rates for Indiana bats may also be attributable to limitations associated with pairing passive acoustic monitoring with automated bat identification software (e.g., BCID). BCID’s default setting requires three or more pulses per file for file identification. Echoclass (US Army Engineer Research and Development Center, Vicksburg, MS), another automated identification software program, also requires ≥3 pulses per file for identification (E. Britzke, US Army Engineer Research and Development Center, personal communication 2013). We were more conservative and required ≥5 pulses per file for identification with BCID. We chose this approach because the capabilities of automated bat identification software in regards to identifying free-flying *Myotis* bats from passive field recordings remains largely untested, and accurately identifying these species by echolocation calls alone is difficult (Broders et al. 2004, Britzke 2013). Our conservative approach with BCID likely resulted in more unknowns than positive Indiana bat identifications, which influenced detection and occupancy estimates. However, we argue that it is better to safe-guard against misidentifications and thereby potentially underrepresent Indiana bat occurrence than to draw erroneous conclusions from false-positives.

DETECTION PROBABILITY

We originally expected that clutter would negatively affect the probability of detecting Indiana bats, as vegetation inhibits the transmission of ultrasounds (Broders et al. 2004) and reduces detection rates for bat detectors (Weller and Zabel 2002, Limpens and McCracken 2004). Sapling density was not a significant predictor of detection probability. However, there was a significant positive relationship between detection probability and forest closure (Figure 3), suggesting that Indiana bats were easier to detect in closed-canopy forests. In the southern Appalachian Mountains, detection probabilities for high-frequency bats are positively related to canopy crown volume, which is directly related to canopy closure (O'Keefe et al. 2014*a*). In our study site, mature oak-hickory forests typically had the highest forest closure estimates. These remnant forests generally possessed closed canopies and uncluttered understories free of the invasive Asian bush honeysuckle (*Lonicera maackii*), which is common in our study area. Our ability to record bats was likely less obstructed by understory vegetation in these areas, which are also known foraging grounds for Indiana bats within our study site (Sparks et al. 2005) and house numerous roost structures (O'Keefe et al. 2014*b*). Therefore, it also seems plausible that detection probabilities were greater in these areas simply due to a greater abundance of individuals (Royles and Nichols 2003) and, hence, greater activity levels.

We observed a significant positive relationship between detection probabilities and mean nightly temperature (Figure 3). While the rate at which sound attenuates in air is directly related to increases in temperature (Griffin 1971), an increase of 15°C has little effect on the attenuation of bat sounds (Lawrence and Simmons 1982). Consequently, the positive relationship we observed is likely related to increased bat activity during warmer temperatures (O'Farrell et al. 1967, Negraeff and Brigham 1995, Erickson and West 2002) resulting from reduced thermoregulation constraints and increased insect prey abundance (Anthony et al. 1981). Warmer temperatures also coincide with adults lengthening their foraging bouts in an effort to build fat reserves for the upcoming winter (Seidman and Zabel 2001) and an increase in the number of individuals out foraging after juveniles become volant (Maier 1992, Whitaker and Sparks 2008). Thus, with a larger number of individuals flying and increased activity levels later in the summer, the probability of detecting Indiana bats should hypothetically increase (Royle and Nichols 2003, Tanadini and Schmidt 2011). This may also explain why we observed a non-significant positive relationship between probability of detection and date of sampling (Table 5). Bat activity is highly variable and can differ substantially between nights (Hayes 1997); thus, the detectability of Indiana bats will likely be influenced by the date acoustic sampling is conducted (Robbins et al. 2008, Romeling et al. 2012). In both 2012 and 2013, Indiana bats were recorded more often following the onset of juvenile volancy (i.e., ~ early to mid-July; O'Keefe et al. 2012, 2014*b*; Table 3) and by mid- to late-July we typically observed the highest emergence counts (e.g., ≥150 bats) for the primary maternity colony (O'Keefe et al. 2012, 2014*b*).

SITE OCCUPANCY

With the exception of distance to agriculture, none of the covariates for probability of occupancy significantly influenced Indiana bat occupancy within our study site. However, our models were likely underpowered due to limited detections of Indiana bats. Surveying more sites or sampling more nights per site would likely increase the number of detections (Gorresen et al. 2008). We may have obtained different results with higher detection rates and, thus, our results should be interpreted with caution.

We detected Indiana bats in every land-cover type we sampled (Table 2), which corresponds with earlier findings from our study site (Sparks et al. 2005, Whitaker et al. 2011). In a radio telemetry study, Sparks et al. (2005) found that Indiana bats foraged in a variety of habitats within our study site, but most often in forests and agricultural lands. In fact, agricultural lands made up ~51% of Indiana bats' foraging ranges, though Indiana bats used forests more often than expected based on their availability (Sparks et al. 2005). Likewise, we observed that distance to agriculture was a significant predictor of occupancy (Table 7), and occupancy rates for Indiana bats were higher nearer to agricultural lands (Figure 4). Indiana bats were detected via acoustics (this study) and observed foraging (via telemetry) almost exclusively south of I-70 (O'Keefe et al. 2012, 2014*b*), an area containing the bulk of forests and agricultural lands within our study site (Figure 1). Foraging Indiana bats were commonly tracked moving between forests and agricultural lands in this area (Whitaker et al. 2011, O'Keefe et al. 2012, O'Keefe et al. 2014*b*), suggesting that these bats may forage in both habitats or Indiana bats may be targeting forest-agricultural edges (Brack 1983, Wolcott and Vulinec 2012). Edges may support more insects (Grindal and Brigham 1999, Verboom and Spoelstra 1999), and linear edges between agricultural lands and other cover types may aid in orientation and serve as commuting corridors for Indiana bats within this very fragmented study site (Murray and Kurta 2004).

Overall, we are uncertain whether agriculture lands are important foraging grounds for Indiana bats within this study site. Data from the same site indicate that Indiana bats forage over agricultural lands (Sparks et al. 2005) and eat several types of crop pests (Tuttle et al. 2006). On the other hand, in other parts of the Eastern and Midwestern United States, Indiana bats forage primarily in forested areas or in riparian/wetland habitats near or within forests (Humphrey et al. 1977, Kessler et al. 1981, Bowles 1981, Brack 1983, Murray and Kurta 2004, Carter 2006). Furthermore, in an agriculture-dominated landscape in Michigan that was similar to our study site, Indiana bats foraged primarily in forests (>90% of foraging activity) even though agricultural lands were prevalent (~60% of the study area; Murray and Kurta 2004). In the present study, acoustic sampling was limited strictly to edge habitat near agricultural lands; we suggest additional sampling near the center of agricultural lands to determine if this cover type serves as foraging grounds. Regardless, within our study site, it appears that Indiana bats may be opportunistic foragers (Menzel et al. 2001) and non-forested habitats likely provide resources not found in other cover types (Brack 2006, Sparks et al. 2005, O'Keefe et al. 2014*b*, Yates and Muzika 2006).

We expected that proximity to site-specific landscape features and habitat types would influence site occupancy for foraging Indiana bats, but our results did not support this expectation. Overall, we detected Indiana bats most often in riparian/wetland areas, followed by deciduous forests; however, ~60% of sampled points occurred in these two land-cover types (Table 2). Riparian and other hydric land-cover types (e.g., wetlands) located within or near forests are important foraging areas for Indiana bats in the Midwest (Kurta and Whitaker 1998, Murray and Kurta 2002, Murray and Kurta 2004, Carter 2006, Bergeson et al. 2013). In our study area, the Indiana bat maternity colony roosts predominantly in trees or bat boxes that occur within or near riparian/wetland areas (Whitaker et al. 2006, O'Keefe et al. 2012). We expected Indiana bats would be detected more often near maternity roosts due to the foraging/nursing obligations of lactating females (Clark et al. 2002, Murray and Kurta 2004). In southern Illinois, for example, Indiana bat foraging ranges are small (285 ± 32 ha: 95% fixed kernel) and bats tend to forage in close proximity to roosting areas in bottomland hardwood forests (Bergeson et al. 2013). However, in this study, neither proximity to riparian/wetlands and deciduous forests nor microhabitat characteristics related to roost site selection (e.g., number of snags, number of live trees with diameters ≥ 30 cm, and number of shagbark hickories; Whitaker et al. 2011, O'Keefe et al. 2014*b*) affected occupancy for Indiana bats. In our study area, bats may need to forage farther from roosting areas because suitable foraging habitat may be limited due to habitat alteration and human disturbance (Sparks et al. 2005). We note that much of our sampling was conducted within a relatively short distance (< 3 km) of the maternity roosts, so perhaps we were limited in our ability to detect an effect of proximity to land-cover types suitable for maternity roosts.

IMPLICATIONS

Detection rates for Indiana bats were relatively low in relation to our sampling effort and proximity to a concentrated population. In the Midwest, Indiana bats are thought to be well-adapted to fragmented landscapes (Brack and Whitaker 2006) and capable of exploiting resources in a variety of land-cover types. This presents a dilemma for surveyors, as the effectiveness of different sampling techniques (e.g., mist-nets and bat detectors) may vary by cover type. For example, acoustic surveys may be more appropriate in uncluttered, open cover types (e.g., grasslands or agricultural lands) where mist-netting would be unproductive. However, our low detection rates suggest that bat detectors may under-sample Indiana bats when present. Detectors only record a subset of emitted bat calls (Adams et al. 2012); pairing this fact with the rarity of Indiana bats on the landscape and the short distance their high-frequency calls travel, we conclude that 2 nights of passive acoustic sampling per site may be insufficient for reliably detecting this species. One way to mitigate for the rarity of Indiana bats is to increase sampling efforts (e.g., more detector-nights or more detectors per area). The current level of effort required in the 2014 US Fish and Wildlife Service Indiana bat summer survey protocol (USFWS 2014) may be insufficient, and we believe further research (e.g., Romeling et al. 2012) is needed to evaluate whether increased acoustic sampling efforts are required to accurately document presence/probable absence. However, we believe that implementing multiple survey methods simultaneously would likely be the best approach, as acoustic and mist-net surveys could be geared toward cover types in which they are most effective. Furthermore, a simultaneous multi-method approach would reduce sampling biases inherent to both survey techniques and enhance the probability of detecting this endangered species. Gaining a better understanding of the distribution and ecology of Indiana bats is of utmost importance due to the severe and ongoing threats (e.g., habitat loss and white-nose syndrome) faced by this rare bat.

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TABLES

Table 1. Covariates used in probability of detection (p) and site occupancy (ψ) models for acoustic data for Indiana bats. Covariates categories were based on the hypothesis being tested. “Forest closure” was derived from the principal component analysis and contained mean canopy closure, mean mid-story closure, and number of trees ≥10 cm DBH in the vegetation plot. Acoustic surveys were conducted near the Indianapolis International Airport, central Indiana, May-August 2012 and 2013.

Covariate Category	***p* covariates**	***ψ* covariates**
Atmospheric Attenuation	Mean Nightly Humidity (% relative) Mean Nightly Temperature (°C) Mean Nightly Wind Speed (km/hr)	
Clutter	"Forest Closure" (FC) # of Saplings (# stems/0.02 ha)	"Forest Closure" (FC) # of Saplings (# stems/0.02 ha)
Temporal	Date of Sampling (DOS)	
Distance (m) to Landscape Features		Water Paved Road Habitat Edge Primary Maternity Roost
Microhabitat		# of Snags (#/0.07 ha) # of Trees >30cm DBH (#/0.07 ha) # of Shagbark Hickories (#/0.07 ha)
Distance (m) to Habitat Type		Wetland/Riparian Area Agriculture Forest Grassland/Pasture Replanted Forest

Table 2. Number of acoustic sampling sites per land-cover type per year, overall percent sampling effort per land-cover type, number of sites with Indiana bat detections per land-cover type, and total number of Indiana bat files recorded per land-cover type for an acoustic study conducted near the Indianapolis International Airport, central Indiana, May-August 2012 and 2013.

Land-cover Type	**Sites Sampled in 2012**	**Sites Sampled in 2013**	**Percent of Total Sampling Effort**	**Sites with Indiana Bat Detections**	**Indiana Bat Files Recorded/ Nights Sampled**	**Nights with Indiana Bat Detections/Nights Sampled**
Wetlands/Riparian	16	6	31.0	13	66/43	19/43
Deciduous Forest	9	11	28.2	9	39/40	14/40
Pasture/Grassland	5	10	21.1	4	13/29	5/29
Replanted Forest	5	6	15.5	4	15/22	5/22
Agricultural Lands	0	3	4.2	1	3/6	2/6
Total	35	36	100.0	31	136/140	45/140

Table 3. Number of sites sampled by month and data on Indiana bat detections by month for an acoustic study conducted near the Indianapolis International Airport, central Indiana, May-August 2012 and 2013.

	2012				**2013**			
Month	**Sites Sampled**	**% of 2012 Detections**	**Files Recorded/ Nights Sampled**	**Nights Detected/ Nights Sampled**	**Sites Sampled**	**% of 2013 Detections**	**Files Recorded/ Nights Sampled**	**Nights Detected/ Nights Sampled**
May	10	36.0	31/18	12/18	8	20.0	10/16	2/16
June	12	17.4	15/24	3/24	12	26.0	13/24	4/24
July	10	41.9	36/20	11/20	14	48.0	24/28	7/28
August	3	4.7	4/6	3/6	2	6.0	3/4	3/4
Total	35	100.0	86/68	29/68	36	100.0	50/72	16/72

Table 4. Confidence set for probability of detection (*p*) models based on acoustic surveys for Indiana bats near the Indianapolis International Airport from May-August 2012 and 2013. Confidence models with covariates, number of model parameters (K), -2 log likelihood values, Akaike's Information Criteria adjusted for small sample sizes (AIC_c), difference in AIC_c from the most parsimonious model (ΔAIC_c), and model weights (w_i) are presented.

Model[1]	**K**	**-2LogLikelihood**	**AIC_c**	**ΔAIC_c**	**w_i**
ψ(.), *p*(FC, Temp, Humid)	5	146.29	157.21	0	0.5665
ψ(.), *p*(Global)	8	141.93	160.25	3.04	0.1239
ψ(.), *p*(FC, Saplings)	4	152.13	160.74	3.53	0.0970
ψ(.), *p*(DOS, FC)	4	153.15	161.76	4.55	0.0582

[1] See Table 1 for variable definitions

Table 5. Probability of detection (*p*) covariates, summed covariate model weight (w_i), model-averaged estimates and standard errors, and 85% confidence levels for the confidence set of probability of detection models for an acoustic study of Indiana bats conducted near the Indianapolis International Airport, central Indiana, May-August 2012 and 2013.

				85% Confidence Level	
Covariate[1]	**w_i**	**Estimate**	**Std. Error**	**Lower**	**Upper**
"Forest closure"[2]	0.8456	1.0766	0.6701	0.1117	2.0415
Mean nightly temperature[2]	0.6904	1.1894	0.5930	0.3355	2.0434
Mean nightly humidity	0.6904	-0.5958	0.4181	-1.1978	0.0063
Number of saplings	0.2209	-0.7346	0.5303	-1.4983	0.0290
Date of sampling	0.1821	0.1166	0.4164	-0.4829	0.7162
Mean nightly wind speed	0.1239	-0.1444	0.4044	-0.7268	0.4379
p intercept	-	0.3744	0.4139	-0.2216	0.9705

[1] See Table 1 for variable definitions

[2] Denotes covariate with 85% confidence interval that does not contain zero

Table 6. Confidence set for site occupancy (ψ) models based on acoustic surveys for Indiana bats near the Indianapolis International Airport from May-August, 2012 and 2013. Models with covariates, number of model parameters (K), -2 log likelihood values, Akaike's Information Criteria adjusted for small sample sizes (AIC_c), difference in AIC_c from the most parsimonious model (ΔAIC_c), and model weights (w_i) are presented.

Model[1]	**K**	**-2LogLikelihood**	**AIC_c**	**ΔAIC_c**	**w_i**
ψ(.), *p*(FC,Temp)	4	148.91	157.52	0	0.1303
ψ(Agriculture), *p*(FC,Temp)	5	146.68	157.60	0.08	0.1252
ψ(Replanted), *p*(FC,Temp)	5	146.74	157.66	0.14	0.1215
ψ(Edge), *p*(FC,Temp)	5	148.00	158.92	1.40	0.0647
ψ(Wetlands), *p*(FC,Temp)	5	148.03	158.95	1.43	0.0638
ψ(Saplings), *p*(FC,Temp)	5	148.09	159.01	1.49	0.0619
ψ(FC), *p*(FC,Temp)	5	148.14	159.06	1.54	0.0603
ψ(Water), *p*(FC,Temp)	5	148.30	159.22	1.70	0.0557
ψ(Grasslands), *p*(FC,Temp)	5	148.59	159.51	1.99	0.0482
ψ(Road), *p*(FC,Temp)	5	148.84	159.76	2.24	0.0425
ψ(PrimaryRoost), *p*(FC,Temp)	5	148.88	159.80	2.28	0.0417
ψ(Forests), *p*(FC,Temp)	5	148.91	159.83	2.31	0.0411
ψ(Shags,AltLive), *p*(FC,Temp)	6	147.12	160.43	2.91	0.0304
ψ(FC,Saplings), *p*(FC,Temp)	6	147.39	160.70	3.18	0.0266
ψ(Edge,Road), *p*(FC,Temp)	6	147.57	160.88	3.36	0.0243
ψ(Snags,AltLive), *p*(FC,Temp)	6	147.58	160.89	3.37	0.0242
ψ(Snags,Shags), *p*(FC,Temp)	6	147.90	161.21	3.69	0.0206
ψ(Water,Roosts), *p*(FC,Temp)	6	148.28	161.59	4.07	0.0170

[1] See Table 1 for variable definitions

Table 7. Site occupancy (ψ) covariates, summed covariate model weight (w_i), model-averaged estimates and standard errors, and 85% confidence levels for the confidence set of probability of occupancy models for an acoustic study of Indiana bats conducted near the Indianapolis International Airport, central Indiana, May-August 2012 and 2013.

				85% Confidence Level	
Covariate[1]	w_i	**Estimate**	**Std. Error**	**Lower**	**Upper**
Distance to agricultural[2]	0.1252	-0.4606	0.3141	-0.9129	-0.0082
Distance to replanted forest	0.1215	0.4435	0.3487	-0.0586	0.9456
Distance to habitat edge	0.0890	0.3464	0.4077	-0.2406	0.9335
Number of saplings	0.0885	-0.3542	0.4148	-0.9515	0.2431
"Forest closure"	0.0869	0.8771	0.8976	-0.4155	2.1697
Distance to water	0.0727	-0.2312	0.3086	-0.6756	0.2131
Distance to paved road	0.0668	-0.1335	0.3277	-0.6054	0.3385
Distance to wetlands/riparian	0.0638	-0.2508	0.2710	-0.6409	0.1394
Distance to primary roost	0.0587	0.0443	0.2793	-0.3578	0.4464
Number of alternate live roosts	0.0546	0.3361	0.3661	-0.1911	0.8633
Number of shagbark hickories	0.0510	0.2347	0.3488	-0.2675	0.7370
Distance to pasture/grasslands	0.0482	0.1883	0.3471	-0.3115	0.6882
Number of snags	0.0448	0.0069	0.3062	-0.4340	0.4479
Distance to forest	0.0411	-0.0001	0.3092	-0.4453	0.4451
ψ intercept	-	0.1617	0.3671	-0.3669	0.6904

[1] See Table 1 for variable definitions

[2] Denotes covariate with 85% confidence interval that does not contain zero

FIGURES

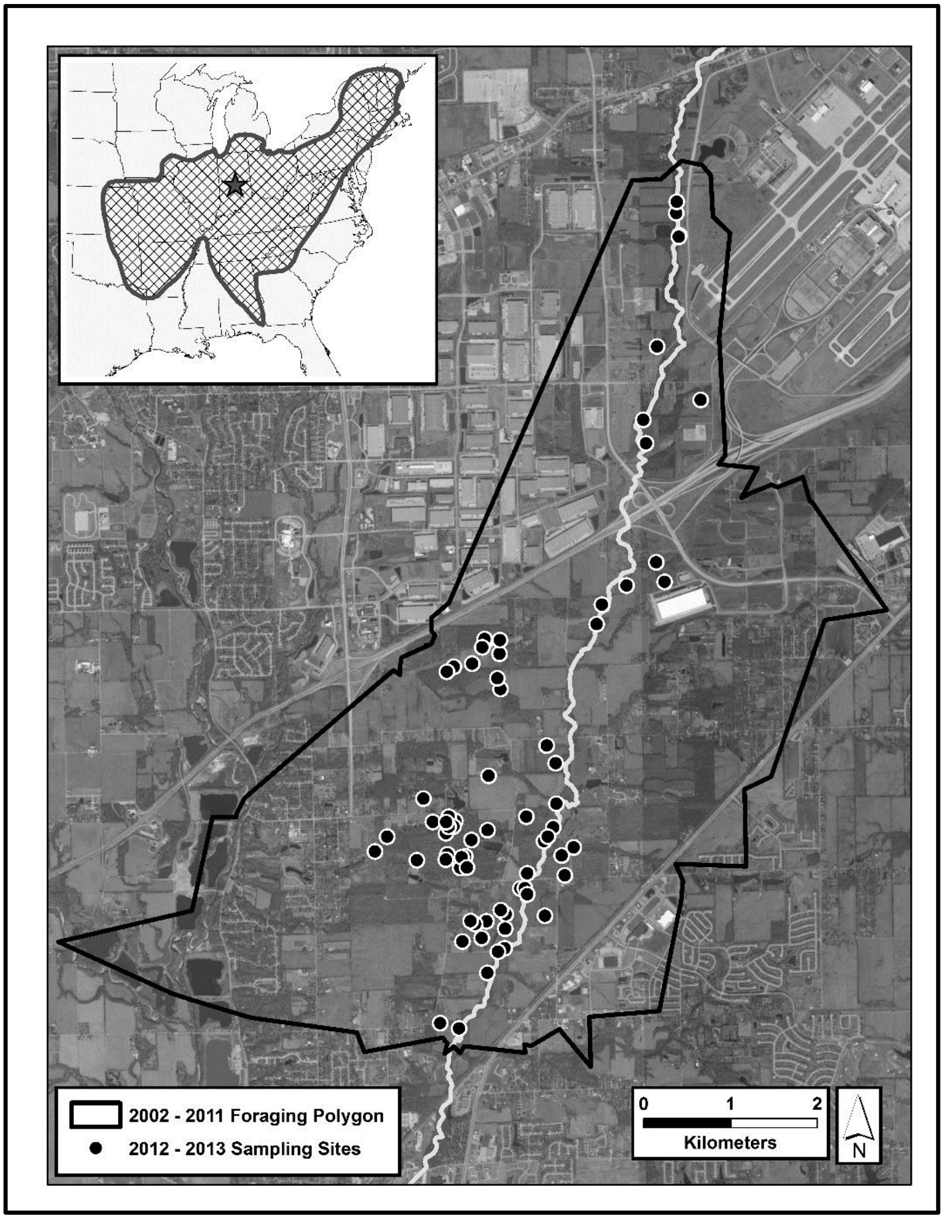

Figure 1. Study area near the Indianapolis International Airport in central Indiana. The inset map shows the study site (star) and a 2013 range map for Indiana bats. The black dots represent 71 acoustic sampling sites surveyed from May-August, 2012 and 2013. The black polygon delineates combined foraging locations for Indiana bats derived from foraging telemetry data from 2002-2011. The grey line running north-south represents the East Fork of White Lick Creek.

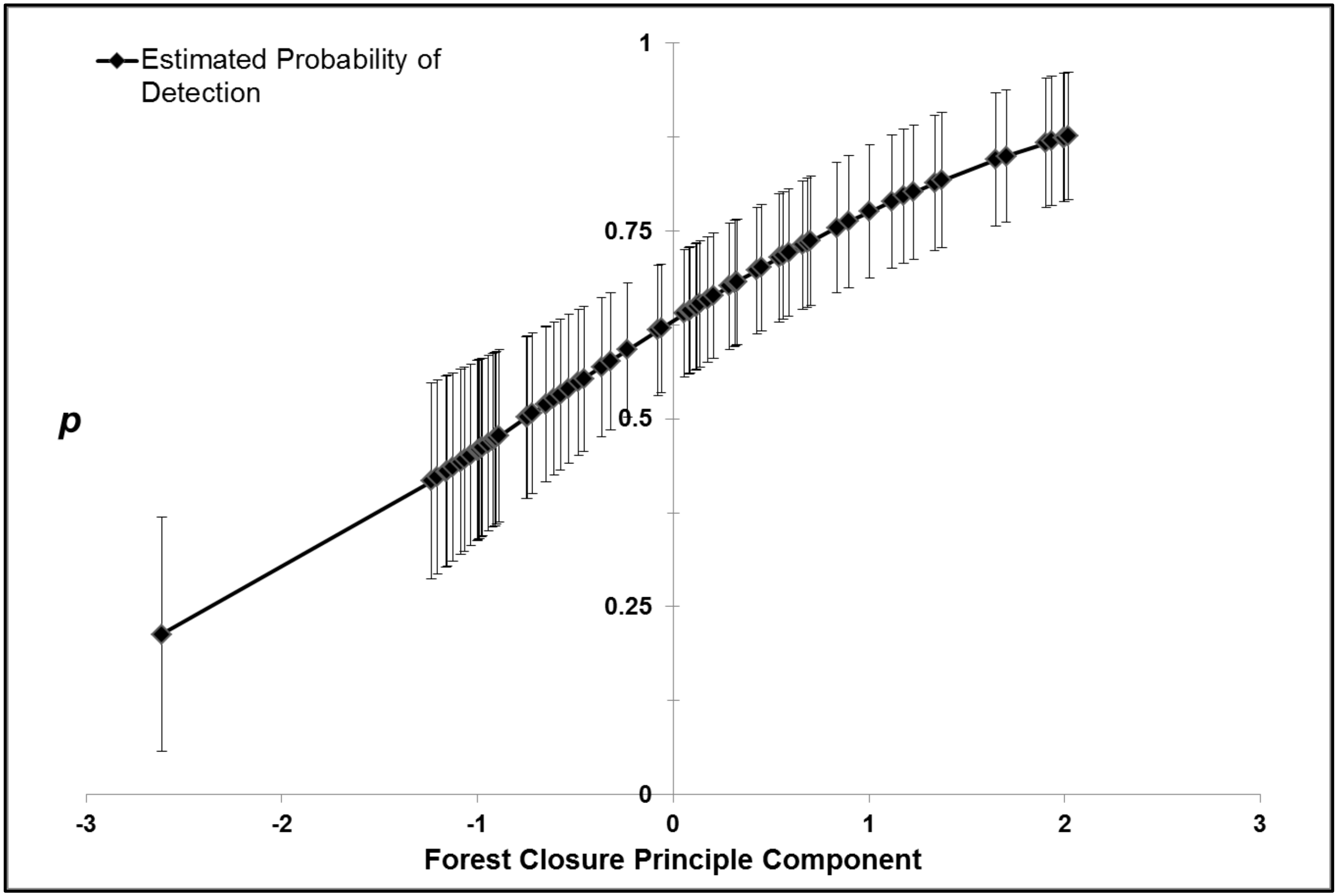

Figure 2. There was a positive relationship between the probability of detecting Indiana bats (*p*) and forest closure. Negative values on the x-axis indicate low forest closure, which was a principal component derived from mean canopy closure, mean mid-story closure, and number of trees ≥10 cm DBH in the vegetation plot. Standard errors are provided for the probability of detection estimates. Acoustic surveys were conducted near the Indianapolis International Airport, central Indiana, May-August 2012 and 2013.

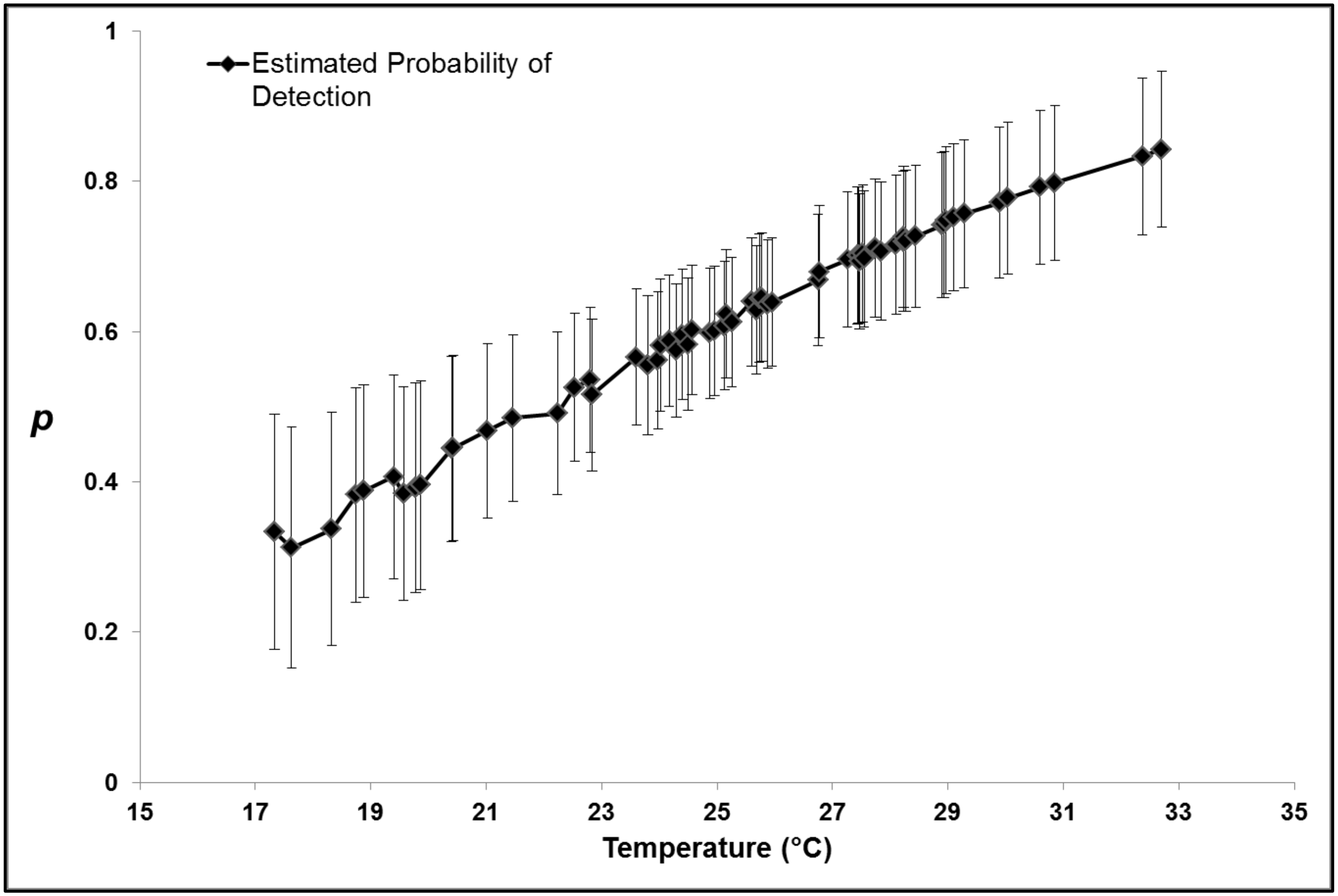

Figure 3. There was a positive relationship between the probability of detecting Indiana bats (*p*) and mean nightly temperature. Standard errors are provided for the probability of detection estimates. Acoustic surveys were conducted near the Indianapolis International Airport, central Indiana, May-August 2012 and 2013.

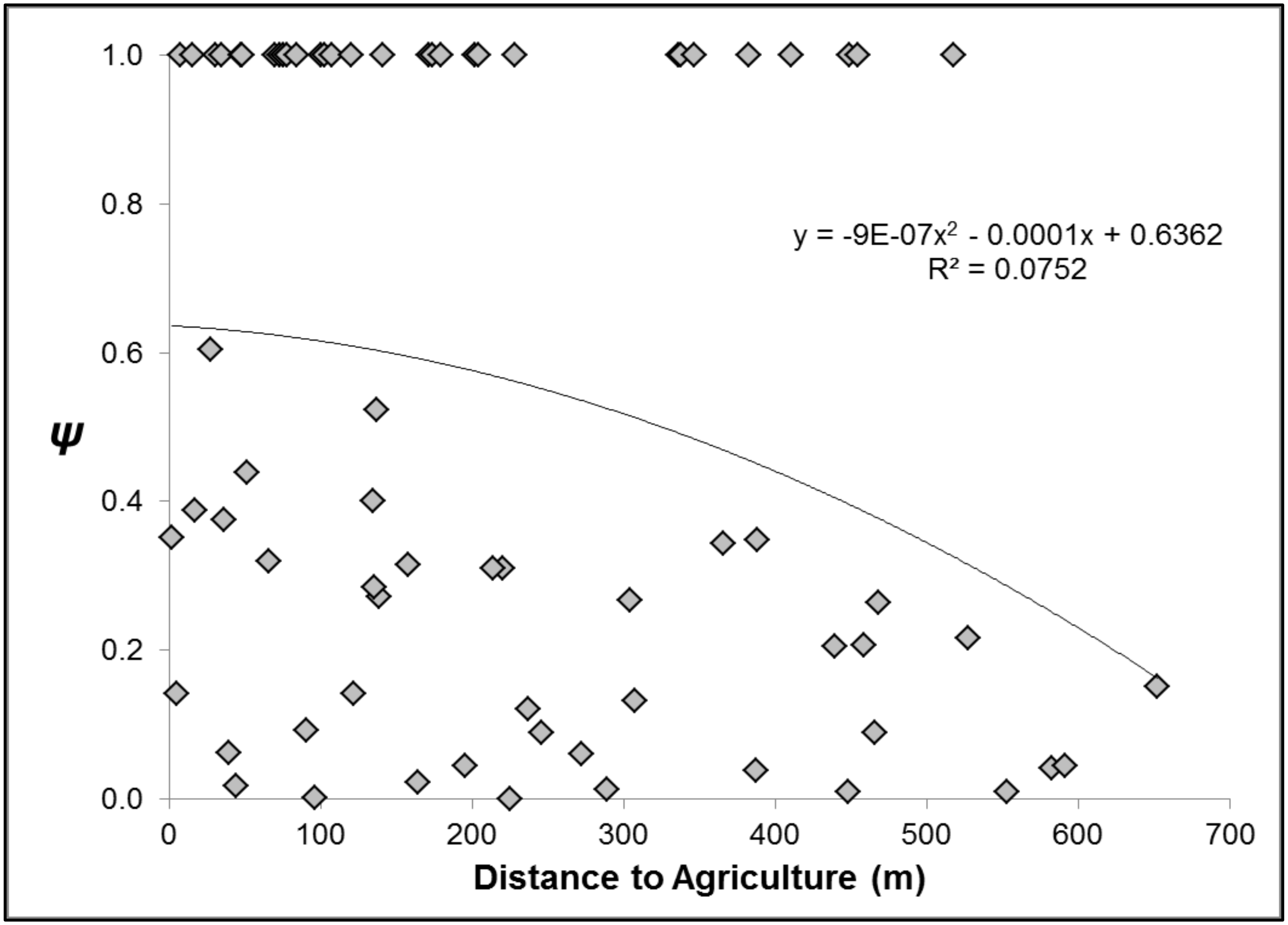

Figure 4. There was a negative relationship between site occupancy for Indiana bats (*ψ*) and distance to agriculture. Acoustic surveys were conducted near the Indianapolis International Airport, central Indiana, May-August 2012 and 2013. Trendline was added with Microsoft Excel 2010.

APPENDICES: PROBABILITY OF DETECTION AND SITE OCCUPANCY MODELS WITH COVARIATE RANGES

Appendix 1. List of 15 probability of detection (*p*) models, their covariates, and covariate ranges based on data collected during acoustic surveys for Indiana bats at a study area near the Indianapolis International Airport in central Indiana from May-August, 2012 and 2013.

Model Title	**Included Covariate(s)**	**Covariate Range**
Time of Season	Date of Sampling (DOS)	135-219
Forest Phenology	DOS; Forest Closure[1]	135-219; -2.6-2.0
Sapling Phenology	DOS; # Saplings	135-219; 0-91
Humidity	Mean Nightly Humidity (MNH)	43-91%
Temperature	Mean Nightly Temperature (MNT)	17.3-32.7°C
Wind	Mean Nightly Wind Speed (MNWS)	7.2-23.9 km/hr
All Weather	MNH; MNT; MNWS	43-91%; 17.3-32.7°C; 7.2-23.9 km/hr
Seasonal Weather	DOS; MNH; MNT; MNWS	135-219; 43-91%; 17.3-32.7°C; 7.2-23.9 km/hr
Forest Closure	Forest Closure[1]	-2.6-2.0
Forest Regrowth	Forest Closure[1]; # Saplings	-2.6-2.0; 0-91
Nearby Clutter	# Saplings	0-91
Forest Attenuation	Forest Closure[1]; MNH; MNT	-2.6-2.0; 43-91%; 17.3-32.7°C
Windy Clutter	# Saplings; MNWS	0-91; 7.2-23.9 km/hr
Global	All Covariates	All of the above
Null	Intercepts only	N/A

[1] Forest Closure is a principal component derived from mean canopy closure, mean mid-story closure, and number of trees ≥10 cm DBH in the vegetation plot

Appendix 2. List of 18 site occupancy (*ψ*) models, their covariates, and covariate ranges based on data collected during acoustic surveys for Indiana bats at a study area near the Indianapolis International Airport in central Indiana from May-August, 2012 and 2013.

Model Title	**Included Covariate(s)**	**Covariate Range**
Nearest Water	Distance to water	0.5-997.9 m
Nearest Primary Roost	Distance to primary roost	194.7-8389.1 m
Nearest Edge	Distance to edge	0-148.2 m
Nearest Road	Distance to road	20.6-599.2 m
Nearest Disturbance	Distance to edge; Distance to road	0-148.2 m; 20.6-599.2 m
Roost & Water	Distance to water; Distance to primary roost	0.5-997.9 m; 194.7-8389.1 m
Roost Availability	# Snags; # Trees >30cm DBH	0-6; 0-13
Roost Availability 1	# Trees >30 cm DBH; # Shagbark hickories	0-13; 0-23
Roost Availability 2	# Snags; # Shagbark hickories	0-6; 0-23
Forest Closure	Forest Closure[1]	-2.6-2.0
Forest Structure	Forest Closure[1]; # Saplings	-2.6-2.0; 0-91
Nearby Clutter	# Saplings	0-91
Nearest Agriculture	Distance to Agriculture	15.7-652.3 m
Nearest Deciduous Forest	Distance to Forest	0-336.7 m
Nearest Pasture/Grassland	Distance to Pasture/Grassland	0-395.4 m
Nearest Replanted Forest	Distance to Replanted Area	0-1459.2 m
Nearest Wetland/Riparian	Distance to Wetland/Riparian	0-737.0 m
Null	Intercepts only	N/A

[1] Forest Closure is a principal component derived from mean canopy closure, mean mid-story closure, and number of trees ≥10 cm DBH in the vegetation plot