

## **Effects of omnidirectional microphone placement and survey period on bat echolocation call quality and detection probabilities**

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Many factors, including microphone type, affect the quality of acoustic calls recorded by bat detectors and detection probabilities of individual species. Because omnidirectional microphones tend to have a shorter range and record more noise than directional microphones, it has been suggested that these microphones be set farther from reflecting surfaces. Our objective was to determine the effects of microphone height (1.5, 5, and 9 m), distance from forest edge (1, 3, and 5 m), and survey timing on the number of bat files recorded, quality of recorded files, the proportion of identifiable files, and the probability of detecting individual species. We deployed 3×3 arrays of two types of bat detectors with omnidirectional microphones at two sites in Kentucky during two survey periods. We found little evidence for effects of microphone height or distance from forest edge on call quality or detection probabilities of any species. In contrast, survey period significantly affected the number of files recorded, the proportion of high-quality files, the proportion of identifiable files, and the probability of detecting individual species; the length of the recording session also significantly affected the probability of detecting some species. Thus, it appears that biologists have some latitude when placing detectors with omnidirectional microphones on the landscape but timing of surveys should be considered when designing and analyzing bat acoustic survey and monitoring studies.

*Key words:* Indiana bat, *Myotis sodalis*, detection probabilities, omnidirectional microphones, acoustic surveys, clutter, survey timing

### INTRODUCTION

Over the past two decades acoustic detectors have become a common means to survey and monitor bats at local to regional scales (Britzke *et al.*, 2013). Because populations of some cave-hibernating bats have declined precipitously in the eastern U.S. in response to white-nose syndrome (WNS), use of mist-nets to determine presence of bats on the landscape and use of various habitats has become extremely inefficient (Francl *et al.*, 2012; Moosman *et al.*, 2013; Pettit and O’Keefe, 2017b). Thus, acoustic surveys have gained even more importance for studying bat distributions and habitat use in recent years. For example, prior to 2012 regulatory surveys to determine the presence or probable absence of the endangered Indiana bat (*Myotis sodalis*) required the use of mist-netting (U.S. Fish and Wildlife Service, 2007). However, in 2012 acoustic surveys were incorporated into the Indiana bat survey protocol and can now be used instead of, or in

conjunction with, mist-net surveys to determine presence/probable absence in most states (U.S. Fish and Wildlife Service, 2018).

Compared to mist-netting and other capture methods, acoustic surveys are relatively easy to conduct, require fewer personnel, and are less invasive (Parsons and Szewczak, 2009). However, knowledge of the biology of the bats in the community of interest, particularly their echolocation and foraging behavior, and the basics of acoustic detectors greatly increases the probability of obtaining high quality calls (Britzke *et al.*, 2013). For example, many factors can affect the quality of acoustic calls that are recorded and the probability of detecting individual species (Ratcliffe and Jakobsen, 2018). These include detector height (Kalcounis *et al.*, 1999; Menzel *et al.*, 2005; Collins and Jones, 2009; Staton and Poulton, 2012), orientation relative to clutter (Weller and Zabel, 2002), weatherproofing (Britzke *et al.*, 2010), microphone orientation relative to horizontal (Weller and Zabel, 2002; Britzke *et al.*, 2010), and

detector and microphone types (Adams *et al.*, 2012; Kaiser and O’Keefe, 2015a; Ratcliffe and Jakobsen, 2018).

Microphones may be either directional or omnidirectional. The cones of detection for the two types of microphones differ considerably with the directional microphone having a longer cone of detection and the omnidirectional microphone having a shorter but much broader one (Fig. 1). Because omnidirectional microphones can detect bats above and below the axis of the microphone as well as directly in front of it, the volume of space they sample may be greater than that of directional microphones. However, omnidirectional microphones tend to have a shorter range (Fig. 1) and therefore, are less likely to detect bats that are farther from the microphone than a directional microphone (Limpens and McCracken, 2004). Further, because omnidirectional microphones pick up sound waves from below the microphone as well as in front and above it, they are also more likely to pick up echoes or reflections from ground surfaces such as still water or pavement which can greatly distort recorded calls (Parsons and Szewczak, 2009) and noise from rustling vegetation (Kaiser and O’Keefe, 2015a). For example, Wildlife Acoustics SM2BAT+ bat detectors with omnidirectional SMX-US microphones record more noise and experience more distortion than Anabat SD2 detectors with directional microphones (Kaiser and O’Keefe, 2015a). Increasing height or distance from clutter may reduce the amount of noise that omnidirectional microphones record. However, Kaiser and O’Keefe (2015a) found that raising microphones

from 2 m to 5 m in height did not reduce the amount of noise recorded by SMX-US omnidirectional microphones.

Although there are some guidelines on the placement of bat detectors in relation to distance from clutter and height above ground, these guidelines are often general and are not based on empirical data (e.g., Loeb *et al.*, 2015). If detectors with omnidirectional microphones are to be used in regulatory presence/probable absence surveys as well as studies examining bat distributions, habitat use, response to management activities, and changes in relative activity over time, better guidelines are needed on the placement of these detectors in relation to the area immediately surrounding the detectors and height above ground. Our objective was to determine the effects of three detector heights (1.5, 5, and 9 m) and three distances from a forest edge (1, 3, and 5 m) on: 1) the quality of calls recorded, 2) the proportion of identifiable calls, and 3) the probability of detecting individual species. Because we were particularly interested in the ability of omnidirectional microphones to record the federally-listed Indiana bat, we conducted our study in areas near Indiana bat maternity colonies. Further, insect noise can be particularly loud later in the summer in U.S. eastern forests. Thus, we also tested whether the period of the summer when surveys are conducted has a significant effect on the quality of calls recorded, the proportion of identifiable calls, and the probability of detecting individual species. We hypothesized that the proportion of high quality call files and files that could be identified to species would increase with

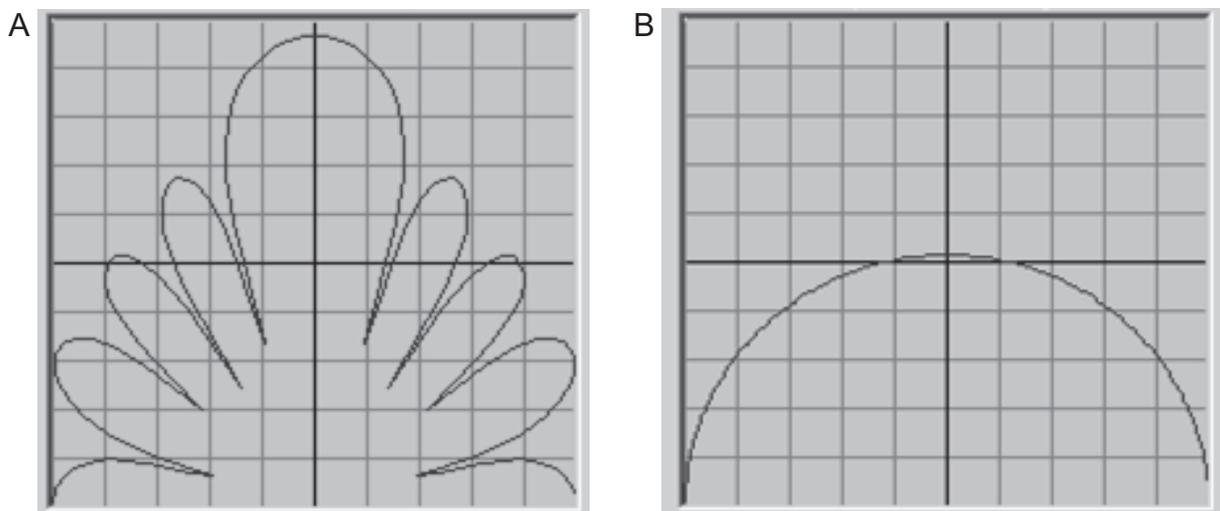


FIG. 1. Theoretical cones of detection for a 45 kHz sound for A — an Anabat SD2 with a directional microphone, and B — an Anabat Express with an omnidirectional microphone. Maximum detection distance and volumes for the directional microphone are 40 m and 24,200 m<sup>3</sup> and 23 m and 22,100 m<sup>3</sup> for the directional and omnidirectional microphones, respectively. Graphic courtesy of Chris Corben

distance from the edge and height above ground. We also predicted that probability of detecting open space bats such as big brown bats (*Eptesicus fuscus*), silver-haired bats (*Lasionycteris noctivagans*), hoary bats (*Lasiurus cinereus*), and gray bats (*Myotis grisescens*) would increase with distance from forest edge and microphone height and that there would be no effect of distance from forest edge and detector height on clutter tolerant and edge-adapted species such as red bats (*Lasiurus borealis*), small-footed bats (*Myotis leibii*), little brown bats (*Myotis lucifugus*), northern long-eared bats (*Myotis septentrionalis*), Indiana bats, evening bats (*Nycticeius humeralis*), and tri-colored bats (*Perimyotis subflavus*). We predicted that the proportion of high-quality calls, the proportion of identifiable calls, and the probability of detecting species would be greater earlier in the summer (late June/early July) than in August.

## MATERIALS AND METHODS

### Study Area

The study was conducted at the Veteran's Memorial Wildlife Management Area (VMWMA) and Fort Knox Military Installation (Fort Knox). VMWMA was located in Scott County, Kentucky and consisted of approximately 1,010 ha of mixed hardwood forest, open fields, and ponds. An Indiana bat maternity colony roost tree was located at VMWMA in summer 2013 and 2014. The Fort Knox study area was located in Bullitt, Hardin, and Meade Counties, Kentucky. The base was comprised of 44,111 ha of mixed hardwood forest, streams, open fields, residential and office areas, and troop training areas. The study area was located in a hunting area which was approximately 445 ha of forest, wetlands, beaver ponds, and a wide, grassy pipeline right-of-way. A maternity colony of Indiana bats was confirmed in the area every summer from 2014 through 2018.

### Acoustic Detector Deployments

We used Anabat Express zero-cross bat detectors (Titley Scientific, Inc., Columbia, MO, USA) and Song Meter SM4BAT full spectrum (FS) bat detectors with SMM-U1 microphones (Wildlife Acoustics, Maynard, MA). Both detector types have omnidirectional microphones that are waterproof and require no additional housing to protect them from the rain. Default settings were used for each detector type. Specifically we set the Anabat Express units to record at a division ratio of 8 and at medium to high sensitivity. We set the SM4BAT to a gain of 12 dB, the 16 k High Filter to off, a sample rate of 256 kHz, a minimum duration of 1.5 ms, maximum duration of none, minimum trigger frequency of 16 kHz, a trigger level of 12 dB, a trigger window of three seconds, and a maximum length of 15 seconds. At each site we placed detectors in a 3 × 3 array in an open area that was adjacent to forest cover. At each distance from the edge (1, 3, and 5 m) detectors were set at either 1.5, 5, or 9 m above ground within approximately 3 m of each

other. Omnidirectional microphones were mounted on poles and attached to the detectors using 10–15 m manufacturer cables and oriented perpendicular to the forest edge.

We recorded bats during two survey periods at each site. The first session was June 28 through July 10, 2016 and the second session was August 3 through August 13, 2016. Detectors were programmed to record from 30–60 minutes prior to sunset to 30–60 minutes after sunrise for three to six consecutive nights. However, some detectors malfunctioned on some nights and either did not record or stopped recording partway through the night. If the detector did not function at all during a night, that night was dropped from the analysis. If several hours of data were recorded during the night, the data were used in the detection probability analysis but not in the analyses of call quality (see below) to reduce bias from partial night data on parameters such as total number of calls and number of high quality calls. Data were uploaded to a computer after the session was completed. During some recording sessions, both detector types were deployed simultaneously whereas in other sessions only one detector type was deployed for 3–6 nights and the other detector type was deployed in subsequent nights.

### Call File Analysis

We used Kaleidoscope Pro 4.2 to convert SM4BAT FS calls to zero-cross files and then used a custom filter in AnalookW to remove files that did not contain bat calls. We examined each file that passed this filter to ensure that they contained ≥1 bat call and removed any files that did not contain bat calls. We then used a more stringent filter to remove files with <5 pulses and which contained non-search phase calls (e.g., feeding buzzes, social calls). These files were also examined and files that contained non-search phase calls were deleted. The remaining files were considered high quality (HQ) files. We ran each of the HQ files through Kaleidoscope Pro 4.2 using the 'Balanced/Neutral' setting to determine the number of files that were designated as identifiable. Species that were included in the analysis were big brown bat, silver-haired bat, red bat, hoary bat, gray bat, small-footed bat, little brown bat, northern long-eared bat, Indiana bat, evening bat, and tri-colored bat.

We used the 'Disperse' function in AnalookW to place files into species folders for each detector and night (Reichert *et al.*, 2018) to allow for easy verification of species presence for each detector each night. Although the calls of little brown bats, northern long-eared bats, Indiana bats, and small-footed bats can be distinguished with automated software programs (e.g., Britzke *et al.*, 2002, 2011) differences among species are often subtle. Thus, if a call was identified as a *Myotis* spp. by the program, we verified that it was a *Myotis* (i.e., not a feeding buzz or a red bat in clutter, both of which can be misidentified as a *Myotis*) and used the species identification given by the program. Big brown bat and silver-haired bat calls are very similar in frequency and structure and it is often difficult to distinguish the species based on their calls. Therefore, we combined calls of these two species. Because silver-haired bats were uncommon in both of our study areas (B. A. Hines, unpublished data), it is likely that most of the calls in this group were big brown bats.

### Statistical Analysis

#### Call quality and program identification

We used mixed effects general and generalized linear models (GLM) to determine whether the total number of bat files

(Total), the total number of files with high quality calls (HQ), the proportion of total files that were HQ files (PropHQ), and the proportion of HQ calls that were considered identifiable by Kaleidoscope Pro (PropID) varied among detector distances, heights, and survey periods. Because Total and HQ were counts and the variances were considerably higher than the means, we used Proc Glimmix (SAS ver. 9.4) and assumed a negative binomial distribution with a log link function. We used Proc Mixed to analyze PropHQ and PropID because they exhibited approximately normal distributions. For all models, distance, height, survey period, and their interactions were fixed effects and study area (hereafter area), area\*distance\*height and area\*distance\*height\*survey period were random effects. We did not include detector type in the analysis because we were not interested in differences between detectors and we were limited in the number of variables we could include in the models. Instead we ran the models separately for each detector type. We used  $\alpha \leq 0.05$  to determine statistical significance and report raw or back-transformed least square means and standard errors. We used Tukey's LSD to test for significant differences among least square means when the results of the GLMs indicated significant effects.

### Probability of detection

We used Program Presence ver. 12.7 to test whether probability of detection for each species varied with detector height, distance from the edge, or environmental conditions. Although we surveyed bats during two survey periods (July and August), we used a single season model and included survey period as a covariate. Each night was considered a sampling occasion and a species was considered to be present (1) if we identified at least one high quality file indicative of the species during a particular night at a particular detector or, not detected (0) if we did not following the guidelines of Reichert *et al.* (2018). Although our criterion was at least one high quality file, in most cases there were several high-quality passes for a detector night. We developed six a priori models including the null model to explain detection based on previous studies (Table 1). Covariates included period (June/July or August), distance from forest edge, height of the microphone, and the nightly survey time (minutes). Continuous variables were standardized so that they had a mean of 0 and a standard deviation of 1. We ran correlation analyses to test whether covariates were correlated ( $|r| > 0.7$ ); none of the covariates in our models were correlated.

We used an information theoretic approach to select the best model or models. We tested model fit using the methods

outlined by MacKenzie and Bailey (2004). If the data were over dispersed (i.e.,  $c\text{-hat} > 1$ ) we used the  $c\text{-hat}$  value to estimate QAIC<sub>c</sub> and multiplied standard errors by  $\sqrt{c\text{-hat}}$ . Thus, we report AIC<sub>c</sub> for some species and QAIC<sub>c</sub> for some species. We considered models to be competing if they were within  $2 \Delta\text{AIC}_c$  units of the top model. We defined the 90% confidence set as those models whose Akaike weights summed to 0.90 and used model-averaging to determine the parameter estimates and unconditional standard errors for covariates contained within the 90% model set. We calculated the 85% confidence limits of parameter estimates and considered those with confidence limits that did not include zero to be significant (Arnold, 2010).

## RESULTS

### Call Quality and Program Identification

We recorded 113,484 files that contained  $\geq$  one bat call during 3,275 detector-hours (95,096 files during 1,650 detector-hours at Fort Knox and 18,388 files during 1,625 detector-hours at VMWMA). The mean number of files per night ranged from 113 to 750 and the mean number of high quality files per night ranged from 29 to 333 (Table 2). The total number of files and the number of high quality files tended to be higher at Fort Knox than at VMWMA.

For Anabat Express detectors, neither distance nor height had a significant effect on any of the parameters although there was a significant distance\*survey period interaction for PropHQ (Table 3). PropHQ declined with distance from the edge during the June/July survey period but there was no distance effect during August (Fig. 2). Survey period had a significant effect on Total, PropHQ, and PropID (Table 3). Although PropHQ was significantly greater during the June/July survey period, Total, and PropID were significantly higher during August (Table 4).

For SM4BAT detectors, distance had a significant effect on HQ (Table 3). The number of HQ files

TABLE 1. Model name, covariates in each model, and the range of each covariate in detection probability models for six species of bats at Fort Knox, KY and Veteran's Memorial Wildlife Management Area (VMWMA), June/July and August, 2016. Period was not included in gray bat models

Model name	Covariate names	Covariate range
Period	Survey period	1 (Jun/Jul) – 2 (August)
Survey time	Survey time	60–739 min
Temporal	Survey period	1 (Jun/Jul) – 2 (August)
	Survey time	60–739 min
Placement	Distance	1–5 m
	Height	1.5–9 m
	Distance*Height	
Placement + Temporal	Variables above	
Null	Intercept only	

TABLE 2. Mean (and SE) number of total call files (Total) and high quality call files (HQ) recorded per night with Anabat Express and SM4BAT+ FS detectors at Fort Knox, KY and Veteran’s Memorial Wildlife Management Area (VMWMA), June/July and August, 2016 as well as the mean proportion of high quality calls (PropHQ), and the proportion of calls that were identifiable by Kaleidoscope Pro 4.2 (PropID)

Files/Calls	Anabat Express		SM4BAT	
	Fort Knox	VMWMA	Fort Knox	VMWMA
Total	527.43 (18.95)	112.63 (7.09)	749.76 (34.75)	144.53 (7.01)
HQ	193.40 (8.52)	29.30 (2.27)	332.75 (16.73)	76.25 (4.58)
PropHQ	0.370 (0.010)	0.245 (0.010)	0.446 (0.011)	0.532 (0.021)
PropID	0.639 (0.011)	0.674 (0.018)	0.431 (0.019)	0.286 (0.026)

recorded at 5 m from the edge was significantly lower than the number of HQ files recorded at 1 m or 3 m from the edge (Table 4). Survey period had a significant effect on all parameters except Total (Table 3) and in all cases parameters were significantly higher during the June/July survey period than the August survey period (Table 4).

*Probability of Detection*

Red bats and big brown bats/silver-haired bats were detected at almost every detector during almost every night at both areas and during both periods. Further, although we detected a small number of small-footed bats and northern long-eared bats, the

TABLE 3. Results of mixed effects general linear models for total number of bats calls recorded (Total), the number of high quality calls recorded (HQ), the proportion of calls that were high quality (PropHQ), and the proportion of calls that were considered identifiable (PropID) by Kaleidoscope Pro for call files collected by Anabat Express and SM4BAT detectors at Fort Knox and Veteran’s Memorial Wildlife Management Area (VMWMA) in northern Kentucky, June/July and August 2016

Effect	Anabat Express			SM4BAT		
	<i>d.f.</i>	<i>F</i>	<i>P</i>	<i>d.f.</i>	<i>F</i>	<i>P</i>
Total						
Distance	2, 17	0.54	0.592	2, 15	2.33	0.131
Height	2, 17	0.93	0.413	2, 15	0.95	0.409
Distance*Height	4, 17	2.47	0.084	4, 15	0.84	0.523
Survey period	1, 17	21.17	0.000	1, 15	0.13	0.719
Distance*Survey period	2, 17	0.45	0.646	2, 15	0.16	0.878
Height*Survey period	2, 17	0.25	0.781	2, 15	0.32	0.729
Distance*Height*Survey period	4, 17	0.33	0.856	4, 15	0.05	0.995
HQ						
Distance	2, 8	1.21	0.346	2, 15	4.46	0.031
Height	2, 8	1.62	0.256	2, 15	1.48	0.259
Distance*Height	4, 9	2.96	0.089	4, 15	1.42	0.276
Survey period	1, 9	3.16	0.109	1, 17	8.96	0.008
Distance*Survey period	2, 9	1.90	0.205	2, 15	0.39	0.686
Height*Survey period	2, 9	0.45	0.645	2, 15	0.30	0.744
Distance*Height*Survey period	4, 9	0.38	0.818	4, 15	0.27	0.894
PropHQ						
Distance	2, 18	1.19	0.326	2, 16	0.59	0.565
Height	2, 18	0.94	0.410	2, 16	0.02	0.979
Distance*Height	4, 18	0.73	0.585	4, 16	0.17	0.953
Survey Period	1, 18	11.92	0.003	1, 17	13.88	0.002
Distance*Survey period	2, 18	3.63	0.047	2, 16	0.18	0.835
Height*Survey period	2, 18	0.62	0.548	2, 16	0.02	0.980
Distance*Height*Survey period	4, 18	0.38	0.817	4, 16	0.23	0.920
PropID						
Distance	2, 8	1.57	0.263	2, 124	0.24	0.786
Height	2, 8	0.13	0.883	2, 124	0.48	0.623
Distance*Height	4, 8	2.23	0.151	4, 124	0.34	0.852
Survey period	1, 118	37.82	<0.001	1, 124	82.57	<0.001
Distance*Survey period	2, 119	1.85	0.162	2, 124	0.40	0.673
Height*Survey period	2, 119	0.45	0.636	2, 124	1.54	0.217
Distance*Height*Survey period	4, 119	0.72	0.578	4, 124	0.27	0.895

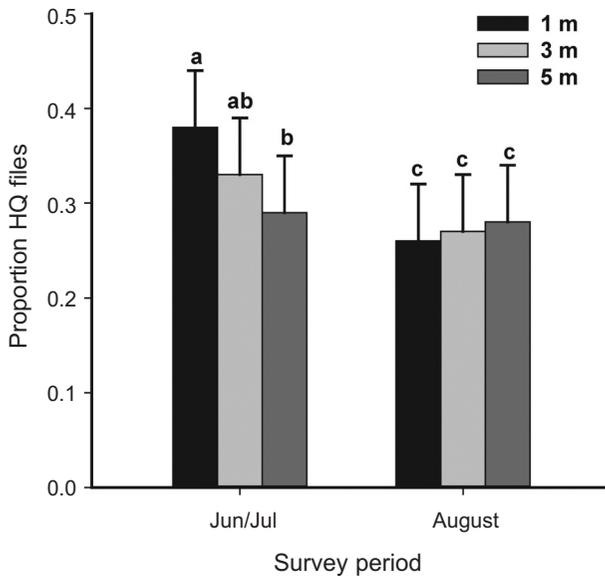


FIG. 2. Proportion of high quality (HQ) files that were recorded at 1, 3, and 5 m from forest edge during June/July and August, 2016 by Anabat Express detectors at Fort Knox and Veterans Memorial Wildlife Management Area. Bars with different letters within a survey period were significantly different ( $P < 0.05$ )

number of detections were insufficient to develop robust detection models. Consequently, many of the models did not converge and several parameter estimates had negative standard errors. Because the models were unreliable, we do not present the results for these four species. Hoary bats were only recorded during the late June/early July survey period and thus, we only used data from this period in our models and excluded Survey Period from our model set as well as from subglobal models that included Survey Period (see Table 1). Further, gray bats were only recorded at Fort Knox and thus, our models were based only on data from that site.

Distance, height, and the distance\*height interaction were only included in the top models for evening bats (Table 5). However, the confidence intervals for the parameter estimates for these variables included zero (Table 6) indicating they had little influence on detection probability. For other species, models that contained distance, height, and their interaction alone performed less well than the null model.

In contrast, survey period or survey time were in the top models for all species (Table 5). Gray bats and evening bats were more likely to be detected in the August survey period whereas little brown bats, Indiana bats, and tri-colored bats were more likely to be detected in late June/early July survey period (Table 6); hoary bats were only detected during the first survey period. Probability of detection also

TABLE 4. Least-square means (and standard errors) of total number of bats calls recorded (Total), the number of high quality calls recorded (HQ), the proportion of calls that were high quality (PropHQ), and the proportion of calls that were considered identifiable by Kaleidoscope Pro (PropID) by Anabat Express and SM4BAT detectors at Fort Knox and Veterans Memorial Wildlife Management Area (VMWMA) in northern Kentucky, June/July and August 2016 at each distance from the edge, detector height, and survey period. Means followed by different letters within a row and category are significantly different ( $P < 0.05$ )

Detector	Distance			Height			Survey period	
	1 m	3 m	5 m	1.5 m	5 m	9 m	Jun/Jul	August
Total								
AE	244.1 (202.11)	237.4 (196.6)	218.1 (180.6)	218.0 (180.6)	253.3 (209.8)	228.7 (189.4)	188.6 (155.9) <sup>a</sup>	287.6 (237.9) <sup>b</sup>
SM4Bat	335.3 (274.4)	341.4 (279.5)	266.8 (218.5)	328.6 (268.9)	282.9 (231.6)	328.6 (269.0)	318.6 (260.3)	306.7 (250.6)
HQ								
AE	76.6 (76.1)	72.2 (71.8)	63.2 (62.8)	65.5 (65.1)	80.3 (79.8)	66.4 (66.0)	63.5 (63.0)	78.2 (77.6)
SM4Bat	174.5 (121.7) <sup>a</sup>	160.1 (111.7) <sup>a</sup>	126.8 (88.4) <sup>b</sup>	157.9 (110.1)	136.9 (95.5)	163.7 (114.2)	174.6 (121.6) <sup>a</sup>	133.0 (92.6) <sup>b</sup>
PropHQ								
AE	0.32 (0.06)	0.30 (0.06)	0.29 (0.06)	0.30 (0.06)	0.32 (0.06)	0.29 (0.06)	0.33 (0.06) <sup>a</sup>	0.27 (0.06) <sup>b</sup>
SM4Bat	0.54 (0.07)	0.49 (0.07)	0.50 (0.07)	0.51 (0.07)	0.51 (0.07)	0.52 (0.07)	0.59 (0.07) <sup>a</sup>	0.43 (0.07) <sup>b</sup>
PropID								
AE	0.64 (0.02)	0.67 (0.02)	0.68 (0.02)	0.66 (0.02)	0.66 (0.02)	0.67 (0.02)	0.60 (0.02) <sup>a</sup>	0.72 (0.02) <sup>b</sup>
SM4BAT	0.36 (0.04)	0.35 (0.04)	0.37 (0.04)	0.35 (0.04)	0.36 (0.04)	0.38 (0.04)	0.48 (0.04) <sup>a</sup>	0.24 (0.04) <sup>b</sup>

TABLE 5. Model, number of parameters (K), Akaike Information Criterion ( $AIC_c$ ) or Quasi Akaike Information Criterion ( $QAIC_c$ ) adjusted for small sample size, difference between the model with the lowest  $AIC_c$  or  $QAIC_c$  and each model's  $AIC_c$  or  $QAIC_c$  ( $\Delta AIC_c$  or  $\Delta QAIC_c$ ), and the model weights ( $\omega_i$ ).  $QAIC_c$  was used for hoary bats, little brown bats, Indiana bats, and tricolored bats

Model	K	$AIC_c$ or $QAIC_c$	$\Delta AIC_c$ or $\Delta QAIC_c$	$\omega_i$
Hoary bats				
p(.)	2	115.23	0	0.506
p(Survey time)	3	115.48	0.136	0.047
p(Placement)	5	121.31	7.466	0.012
p(Placement, Survey time)	6	121.16	8.213	0.008
Gray bats FK Only				
p(Period)	3	158.88	0	0.477
p(Temporal)	4	158.89	0.004	0.476
p(Placement, Temporal)	7	163.52	4.638	0.047
p(Survey time)	3	179.65	20.770	<0.001
p(.)	2	190.30	31.421	<0.001
p(Placement)	5	196.76	37.876	<0.001
Little brown bats				
p(Period)	3	233.23	0	0.593
p(Temporal)	4	235.17	1.924	0.227
p(.)	2	236.56	3.331	0.112
p(Survey time)	3	238.59	5.360	0.041
p(Placement, Temporal)	7	240.36	7.127	0.017
p(Placement)	5	241.21	7.976	0.011
Indiana bats				
p(Period)	3	269.54	0	0.654
p(Temporal)	4	270.97	1.424	0.321
p(Placement, Temporal)	2	276.31	6.797	0.022
p(Survey time)	3	282.22	12.680	0.001
p(.)	7	282.41	12.871	0.001
p(Placement)	5	288.26	18.716	<0.001
Evening bats				
p(Placement, Temporal)	7	306.91	0	0.548
p(Period)	3	308.67	1.763	0.227
p(Temporal)	4	308.70	1.797	0.224
p(Survey time)	3	322.28	15.373	<0.001
p(.)	2	337.76	30.854	<0.001
p(Placement)	5	339.37	32.459	<0.001
Tri-colored bats				
p(Survey time)	3	171.88	0	0.699
p(Temporal)	4	173.73	1.844	0.278
p(Placement, Temporal)	7	180.65	8.767	0.009
p(.)	2	180.52	8.641	0.009
p(Period)	3	181.76	9.880	0.005
p(Placement)	5	186.99	15.106	<0.001

increased with the number of survey minutes per night for gray bats and tri-colored bats.

## DISCUSSION

Although several studies have examined bat activity (i.e., number of call files) in relation to distance from the forest edge and detector height (e.g., Collins and Jones, 2009; Staton and Poulton, 2012; Jantzen and Fenton, 2013; Brooks *et al.*, 2017), to our knowledge, few data are available on the effect of distance from forest edge and height on call quality or probability of detection. Because

omnidirectional microphones are purported to record more noise than directional microphones (Kaiser and O'Keefe, 2015a; Loeb *et al.*, 2015), we predicted that distance from forest edge and height above ground of the omnidirectional microphones would affect the number and quality of bat calls recorded and the ability of the microphones to detect individual species. However, we did not find an effect of either factor on most variables we examined for the two detector types that we tested. Further, the proportion of high quality call files that we recorded (0.25–0.53) was similar to the proportion of high quality calls recorded using directional

TABLE 6. Parameter estimates, standard errors (or model-averaged parameter estimates and unconditional standard errors), and 85% confidence intervals for parameters included in the confidence set of models to predict detection probabilities of bats. Covariates in bold are statistically significant

Parameter	Estimate	SE	85% Confidence interval
Hoary bat			
Intercept	0.296	0.239	-0.048, 0.640
Survey time	0.349	0.240	0.003, 0.695
Gray bat			
Intercept	-3.289	0.676	-4.262, -2.316
Survey time	0.370	0.258	-0.002, 0.742
Period	2.284	0.478	1.596, 2.972
Little brown bat			
Intercept	1.753	0.458	1.094, 2.410
Survey time	0.00002	<0.001	-0.0001, 0.0002
Period	-0.792	0.431	-1.413, -0.171
Indiana bat			
Intercept	2.126	0.633	1.215, 3.038
Survey time	0.191	0.244	-0.160, 0.542
Period	-1.321	0.421	-1.927, -0.715
Evening Bat			
Intercept	-3.283	0.499	-4.002, -2.564
Survey time	0.209	0.151	-0.008, 0.426
Period	1.745	0.595	0.888, 2.602
Distance	-0.338	0.347	-0.838, 0.162
Height	0.166	0.362	-0.355, 0.687
Distance*Height	-0.218	0.474	-0.901, 0.464
Tri-colored bat			
Intercept	0.709	0.559	-0.096, 1.514
Survey time	0.929	0.307	0.487, 1.371
Period	-0.384	0.176	-0.637, -0.131

microphones in similar habitats in Kentucky (0.33–0.52 for detectors with no weather-proofing or ones using a 45° PVC tube for weatherproofing — Britzke *et al.*, 2010). In contrast, survey period affected the number and quality of calls recorded and survey period and survey time affected the probability of detecting individual species and these factors should be taken into consideration when designing acoustic survey and monitoring studies.

With a few exceptions, we found very little evidence for the effect of distance from forest edge on call quality. The proportion of high-quality calls recorded by Anabat Express detectors declined with distance from forest edge but this only occurred during the late June/early July period and the number of high quality calls recorded with SM4BAT detectors was lower at 5 m than at 1 m and 3 m from the forest edge. In both cases, the response was opposite of our prediction. The lack of an effect of distance from forest edge may be due to several factors. It is possible that we may have found a greater effect of distance if we had greater spacing between our detectors (e.g., 1, 5, and 10 m or more from the edge). However, bat activity tends to be highest

close to forest edges and hedgerows and decreases as distance increases (Jantzen and Fenton, 2013; Kelm *et al.*, 2014). Thus, higher activity at the edge may have affected many of our measures even though we tried to control for activity levels by looking at the proportion of high quality and identifiable files. Further, we oriented our microphones perpendicular to the forest edge which may have reduced some of the reflections from the forest vegetation. Thus, our data suggest that setting detectors with omnidirectional microphones approximately 1–3 m from the forest edge is sufficient for collecting high quality calls.

Distance from forest edge also had little effect on the probability of detecting individual species or species groups. We predicted that probability of detecting open space bats such as big brown bats/silver-haired bats, hoary bats, and gray bats would increase with distance from forest edge but that there would be no effect of distance from forest edge for clutter tolerant and edge-adapted species. Distance from the edge and height were only included in the top models for evening bats, and neither distance from the edge, microphone height, or their inter-

action were significant variables in the model. Although activity of species such as big brown bats/silver-haired bats and hoary bats peaks at approximately 10 m from the forest edge in openings in Ontario, Canada (Jantzen and Fenton, 2013), calls of these species may be loud enough that they can be recorded by detectors closer to the edge. In contrast, smaller species such as Indiana bats, little brown, red bats, tri-colored bats, and evening bats are considered to be more closely associated with interior forest or forest edges (Menzel *et al.*, 2005; Jantzen and Fenton, 2013). However, we found that they were as likely to be detected at 5 m from the forest as at 1 m from the forest edge.

Surprisingly, height of the microphone above ground also had little effect on call quality or the ability to identify call files to species in our study. Several studies have found that bat activity or species richness varies with detector microphone height, with some species more active at greater heights and others more active at lower heights (Kalcounis *et al.*, 1999; Menzel *et al.*, 2005; Loeb and Waldrop, 2008; Collins and Jones, 2009; Staton and Poulton, 2012; Froidevaux *et al.*, 2014). We may have not detected a difference among heights because our study was conducted in forest openings whereas many of the studies that detected a difference among heights were conducted within forested habitats and several of these studies compared activity above and below the forest canopy (e.g., Kalcounis *et al.*, 1999; Menzel *et al.*, 2005; Collins and Jones, 2009). Because there was no clutter above our microphones, sound was not obstructed from reaching the microphone, resulting in lower microphones having equal detectability as higher microphones. Further, our highest microphone was only 9-m high whereas other studies have placed detectors as high as 30 m (Menzel *et al.*, 2005; Collins and Jones, 2009). It is possible we may have found differences among heights if we had used 30 m high detectors. However, because placing detectors at 30 m is logistically difficult and often requires the use of existing towers (Kalcounis *et al.*, 1999), telecommunication masts (Collins and Jones, 2009), or suspension of detectors from helium blimps (Menzel *et al.*, 2005) it is unlikely that 30 m sampling heights will be used during routine monitoring. Although we expected lower microphones to pick up more noise, this was not the case. Again, this may be due to the recording habitats which had low ground cover and were in relatively secluded areas keeping noise from vegetation and other sources relatively low. Kaiser and O'Keefe

(2015a) also found that microphone height (2 m versus 5 m) had no influence on the number of bat files recorded with SM2BAT+ detectors with omnidirectional microphones. Thus, at present it does not appear that raising the height of the microphone above 1.5 m (see Weller and Zabel, 2002) will increase the number or proportion of high-quality files recorded by omnidirectional microphones. However, other factors such as the height of the vegetation, the bat community (e.g., the presence of high-flying species), and reflectivity of the ground surface should be taken into consideration when designing acoustic studies of bats in various habitats (Britzke *et al.*, 2013; Loeb *et al.*, 2015).

In contrast to detector height and distance from the edge, survey period was an important parameter in the number of files recorded, the proportion of high-quality files recorded, and the proportion of identifiable files recorded. Because insect noise in eastern U.S. forests is often high during late summer (personal observation) we anticipated that the total number of call files and the quality of call files would be higher during the late June/early July period. Although the total number of bat passes recorded by Anabat Express detectors was greater during the second survey period and the proportion of passes that were identifiable was greater in August for SM4BAT detectors, the total number of high quality call files and proportion of high quality call files recorded by both Anabat Express and SM4BAT detectors were significantly higher during the late June/early July period, supporting our predictions. While other factors such as temperature and humidity may also affect the number of files recorded and call quality (Griffin, 1971), it is likely the high insect noise during the latter part of the summer also influenced our ability to record high quality call files. Although seasonal effects may vary year-to-year or among areas, researchers should be aware that timing of surveys may affect the ability to collect high quality calls.

We also found that survey period was a significant parameter in probability of detecting gray bats, Indiana bats, little brown bats, and evening bats. Further, hoary bats were only recorded during the first survey period. Indiana bats, little brown bats, and tri-colored bats were recorded during both periods but were more likely to be detected during the early summer period whereas detection probabilities of gray bats and evening bats were greater during the late summer period. Differences in detection probabilities among survey periods may be due to species-specific changes in activity during the

summer. For example, in northeastern Missouri, Indiana bats are more likely to be captured and recorded with detectors during the pregnancy period (early summer) whereas evening bats and big brown bats are more likely to be captured or recorded during the lactation and post-lactation period (Robbins *et al.*, 2008). In New York, detection probabilities of red bats, northern long-eared bats, and small-footed bats also increase later in the summer, perhaps due to the higher numbers of individuals as the young become volant (Coleman *et al.*, 2014). However, detection probabilities of Indiana bats do not vary with survey date in Indiana (Kaiser and O'Keefe, 2015b). At our two study sites, activity (based on the number of call files) of Indiana bats during the first survey period was very high at both sites. This was most likely due to the presence of Indiana bats in the maternity roosts near our detectors. Activity of Indiana bats declined as did their detection probabilities in August, most likely due to the breakup of the maternity colonies as the young became volant, the colonies moved to other roosts, or to the onset of migration (Ritzi *et al.*, 2005; Pettit and O'Keefe, 2017a). As the activity of Indiana bats decreased, other species may have moved into the area, thus increasing their probabilities of detection (Jachowski *et al.*, 2014). Because probability of detecting species varies across the maternity season and among species, researchers interested in understanding the occupancy of all species in area may want to consider conducting multiple surveys during the summer. However, if surveys are focused on individual species, surveyors may wish to conduct surveys during periods of the year when those species are most detectable at their site.

Nightly recording time was an important factor explaining detection probabilities of hoary bats and tri-colored bats and the detection probabilities of both species increased with recording time. Neece (2017) also found that survey duration had a significant positive effect on detection probabilities of several species including hoary bats and tri-colored bats. This suggests that every effort should be made to assure that detectors record all night.

Although it is relatively easy to set up and deploy acoustic detectors to survey bats across various spatial scales, many things must be considered during the design phase of acoustic surveys and research studies (Britzke *et al.*, 2013). Researchers need to carefully consider microphone type, placement of the detectors in the field (e.g., habitat types, distance to clutter, and reflective surfaces), microphone orientation, and time of year as well as

the behavior of the bats because all of these factors can affect the number and quality of calls recorded (Ratcliffe and Jakobsen, 2018). The size and shape of the cone of detection relative to a microphone's orientation should also be considered when deploying acoustic detectors, particularly in relation to types of bats that are likely to be recorded (e.g., high-flying bats with high intensity echolocation calls versus gleaning bats with low intensity calls). Although we found few effects of microphone distance from the forest edge or height above ground on the total number of calls recorded, the proportion of high quality calls recorded, the proportion of identifiable calls recorded, or the probability of detecting individual species for the two detectors with omnidirectional microphones that we tested, these results may vary with bat community or habitat type in which the detectors are deployed. Because acoustic surveys are being used more frequently to inform management and conservation throughout the world (e.g., Indiana Bat Survey Protocols, Eurobats, UK National Bat Monitoring Programme, North American Bat Monitoring Program), we encourage further testing of the effects of microphone placement on call quality and probability of detecting species using a variety of detector and microphone types.

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#### LITERATURE CITED

- ADAMS, A. M., M. K. JANTZEN, R. M. HAMILTON, and M. B. FENTON. 2012. Do you hear what i hear? Implications of detector selection for acoustic monitoring of bats. *Methods in Ecology and Evolution*, 3: 992–998.
- ARNOLD, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management*, 74: 1175–1178.
- BRITZKE, E. R., K. L. MURRAY, J. S. HEYWOOD, and L. W. ROBBINS. 2002. Acoustic identification. Pp. 220–224, *in* The Indiana bat: biology: biology and management of an endangered species (A. KURTA and J. KENNEDY, eds.). Bat Conservation International, Austin, TX, 253 pp.
- BRITZKE, E. R., B. A. SLACK, M. P. ARMSTRONG, and S. C. LOEB.

2010. Effects of orientation and weatherproofing on the detection of bat echolocation calls. *Journal of Fish and Wildlife Management*, 1: 136–141.
- BRITZKE, E. R., J. E. DUCHAMP, K. L. MURRAY, R. K. SWIHART, and L. W. ROBBINS. 2011. Acoustic identification of bats in the eastern United States: a comparison of parametric and nonparametric methods. *Journal of Wildlife Management*, 75: 660–667.
- BRITZKE, E. R., E. H. GILLAM, and K. L. MURRAY. 2013. Current state of understanding of ultrasonic detectors for the study of bat ecology. *Acta Theriologica*, 58: 109–117.
- BROOKS, J. D., S. C. LOEB, and P. D. GERARD. 2017. Effect of forest opening characteristics, prey abundance, and environmental factors on bat activity in the Southern Appalachians. *Forest Ecology and Management*, 400: 19–27.
- COLEMAN, L. S., W. M. FORD, C. A. DOBONY, and E. R. BRITZKE. 2014. Effect of passive acoustic sampling methodology on detecting bats after declines from white nose syndrome. *Journal of Ecology and the Natural Environment*, 6: 56–64.
- COLLINS, J., and G. JONES. 2009. Differences in bat activity in relation to bat detector height: implications for bat surveys at proposed windfarm sites. *Acta Chiropterologica*, 11: 343–350.
- FRANCL, K. E., W. M. FORD, D. W. SPARKS, and V. BRACK, JR. 2012. Capture and reproductive trends in summer bat communities in west Virginia: assessing the impact of white-nose syndrome. *Journal of Fish and Wildlife Management*, 3: 33–42.
- FROIDEVAUX, J. S. P., F. ZELLWEGER, K. BOLLMANN, and M. K. OBRIST. 2014. Optimizing passive acoustic sampling of bats in forests. *Ecology and Evolution*, 4: 4690–4700.
- GRIFFIN, D. R. 1971. The importance of atmospheric attenuation for the echolocation of bats (Chiroptera). *Animal Behavior*, 19: 55–61.
- JACHOWSKI, D. S., C. A. DOBONY, L. S. COLEMAN, W. M. FORD, E. R. BRITZKE, and J. L. RODRIGUE. 2014. Disease and community structure: whitenose syndrome alters spatial and temporal niche partitioning in sympatric bat species. *Diversity and Distributions*, 20: 1002–1015.
- JANTZEN, M. K., and M. B. FENTON. 2013. The depth of edge influence among insectivorous bats at forest-field interfaces. *Canadian Journal of Zoology*, 91: 287–292.
- KAISER, Z. D., and J. M. O'KEEFE. 2015a. Data acquisition varies by bat phonic group for 2 types of bat detectors when weatherproofed and paired in field settings. *Wildlife Society Bulletin*, 39: 635–644.
- KAISER, Z. D., and J. M. O'KEEFE. 2015b. Factors affecting acoustic detection and site occupancy of Indiana bats near a known maternity colony. *Journal of Mammalogy*, 96: 344–360.
- KALCOUNIS, M. C., K. A. HOBSON, R. M. BRIGHAM, and K. R. HECKER. 1999. Bat activity in the boreal forest: importance of stand type and vertical strata. *Journal of Mammalogy*, 80: 673–682.
- KELM, D. H., J. LENSKI, V. KELM, U. TOELCH, and F. DZIOCK. 2014. Seasonal bat activity in relation to distance to hedgerows in an agricultural landscape in Central Europe and implications for wind energy development. *Acta Chiropterologica*, 16: 65–73.
- LIMPENS, H. J. G. A., and G. F. MCCrackEN. 2004. Choosing a bat detector: theoretical and practical aspects. Pp. 28–37, in *Bat echolocation research: tools, techniques and analysis* (R. M. BRIGHAM, E. K. V. KALKO, G. JONES, S. PARSONS, and H. J. G. A. LIMPENS, eds.). *Bat Conservation International*, Austin, Texas, 167 pp.
- LOEB, S. C., and T. A. WALDROP. 2008. Bat activity in relation to fire and fire surrogate treatments in southern pine stands. *Forest Ecology and Management*, 255: 3185–3192.
- LOEB, S. C., T. J. RODHOUSE, L. E. ELLISON, C. L. LAUSEN, J. D. REICHARD, K. M. IRVINE, T. E. INGERSOLL, J. T. H. COLEMAN, W. E. THOGMARTIN, J. R. SAUER, *et al.* 2015. A plan for the North American Bat Monitoring Program (NABAT). Gen. Tech. Report srs-256. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, NC, 100 pp.
- MACKENZIE, D. I., and L. L. BAILEY. 2004. Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics*, 9: 300–308.
- MENZEL, J. M., M. A. MENZEL, JR., J. C. KILGO, W. M. FORD, J. W. EDWARDS, and G. F. MCCrackEN. 2005. Effect of habitat and foraging height on bat activity in the coastal plain of South Carolina. *Journal of Wildlife Management*, 69: 235–245.
- MOOSMAN, P. R., JR., J. P. VEILLEUX, G. W. PELTON, and H. H. THOMAS. 2013. Changes in capture rates in a community of bats in New Hampshire during the progression of white-nose syndrome. *Northeastern Naturalist*, 20: 552–558.
- NEECE, B. D. 2017. North American Bat Monitoring Program (NABAT) in South Carolina: acoustic detection and landscape occupancy of bats. M.Sci. Thesis, Clemson University, Clemson, South Carolina, 92 pp.
- PARSONS, S., and J. M. SZEWCZAK. 2009. Detecting, recording, and analyzing the vocalizations of bats. Pp. 91–111, in *Ecological and behavioral methods for the study of bats*, 2nd edition (T. H. KUNZ and S. PARSONS, eds.). Johns Hopkins University Press, Baltimore, MD, 901 pp.
- PETTIT, J. L., and J. M. O'KEEFE. 2017a. Day of year, temperature, wind, and precipitation predict timing of bat migration. *Journal of Mammalogy*, 98: 1236–1248.
- PETTIT, J. L., and J. M. O'KEEFE. 2017b. Impacts of white-nose syndrome observed during long-term monitoring of a mid-western bat community. *Journal of Fish and Wildlife Management*, 8: 69–78.
- RATCLIFFE, J. M., and L. JAKOBSEN. 2018. Don't believe the mike: behavioural, directional, and environmental impacts on recorded bat echolocation call measures. *Canadian Journal of Zoology*, 96: 283–288.
- REICHERT, B. E., C. LAUSEN, S. LOEB, T. WELLER, R. ALLEN, E. BRITZKE, T. HOHOFF, J. SIEMERS, B. BURKHOLDER, C. HERZOG, and M. VERANT. 2018. A guide to processing bat acoustic data for the North American Bat Monitoring Program (NABAT). U.S. Department of Interior, U.S. Geological Survey, Reston, VA, 59 pp.
- RITZI, C. M., B. L. EVERSON, and J. O. WHATAKER, JR. 2005. Use of bat boxes by a maternity colony of Indiana myotis (*Myotis sodalis*). *Northeastern Naturalist*, 12: 217–220.
- ROBBINS, L. W., K. L. MURRAY, and P. M. MCKENZIE. 2008. Evaluating the effectiveness of the standard mist-netting protocol for the endangered Indiana bat (*Myotis sodalis*). *Northeastern Naturalist*, 15: 275–282.
- STATON, T., and S. POULTON. 2012. Seasonal variation in bat activity in relation to detector height: a case study. *Acta Chiropterologica*, 14: 401–408.
- U.S. FISH AND WILDLIFE SERVICE. 2007. Indiana bat (*Myotis*

- sodalis*) draft recovery plan: first revision. USFWS, Fort Snelling, MN, 258 pp.
- U.S. FISH AND WILDLIFE SERVICE. 2018. Range-wide Indiana bat survey guidelines. Available from <https://www.fws.gov/midwest/endangered/mammals/inba/surveys/pdf/2018rangewideibatsurveyguidelines.pdf>. Accessed February 17, 2019.
- WELLER, T. J., and C. J. ZABEL. 2002. Variation in bat detections due to detector orientation in a forest. *Wildlife Society Bulletin*, 30: 922–930.

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